PALEOGNATHOUS BIRDS
FROM THE EARLY TERTIARY
OF THE NORTHERN HEMISPHERE

PETER W. HOUDE

NUTTALL ORNITHOLOGICAL CLUB
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INTRODUCTION

The recent discovery of paleognathous carinate birds in Tertiary deposits of North America (Houde and Olson, 1981) sheds new light on some long-known, but misunderstood, fossil birds and dramatically illustrates that there are great deficiencies in our comprehension of avian evolution. Some isolated bones of these fossil paleognathous birds are superficially more similar to a number of neognathous carinates than they are to any modern paleognathous birds. Consequently, their true identities have both eluded and confounded taxonomists for more than a century, despite what turns out to be relatively good representation in museum collections. It is doubtful that anyone could have recognized these as paleognathous birds from the fragmentary material from which they were generally known. Elucidation of this systematic tangle results from improved techniques of collecting fossils, specifically by acid etching calcareous nodules. The importance of these birds to the general state of knowledge of early Tertiary ecosystems cannot be overemphasized. These paleognaths represent a major constituent of the early Tertiary avifauna of North America and Europe, from which there are some periods with no previously described fossil birds whatsoever.

In this paper, the fossil paleognathous birds are named, described, and diagnosed. Incorrect descriptions of some of these fossils are revised. I present conclusions about their functional anatomy, behavior, and ecology, and I have proposed some hypotheses to account for their intrafamilial and inter-ordinal relationships. In attempting to achieve these goals, some stages in the early evolution of birds are documented.

CHARACTERISTICS OF PALEOGNATHOUS BIRDS

Modern birds, subclass Neornithes, are divisible into two superorders, the Palaeognathae and Neognathae. The Palaeognathae are so-called for the presumably reptile-like configuration of their bony palate (Pycraft, 1900). In a different taxonomic scheme, the Neornithes are divisible into the Ratitae and Carinatae. Ratites are flightless birds and the name generally applies only to paleognathous birds. Carinates are so termed because they possess keeled breastbones (carinate sterna) for the attachment of their large and powerful breast muscles (pectoralis and supracoracoideus). The neogna-thous character state of the palatal complex of bones is more diagnostic of the Carinatae, however, because some have become flightless and lost the carinae of their sterna (Pycraft, 1900). Moreover, the tinamous (Tinamidae) are paleognathous birds that also exhibit the carina sterni.

Although the paleognathous palate is considered by some (e.g., McDowell, 1948) to be undefinable in that there are several variations of it exhibited by birds, others disagree. Bock (1963) enumerated several osteolog-ical characters that he considered collectively to diagnose the paleognathous

palate. Regardless of which view is correct, the paleognathous palate, together with rhamphothecal grooves (Parkes and Clark, 1966) and the open ilioischiadic foramen (Cracraft, 1974), has gained wide acceptance by the ornithological community as uniting the birds that possess these traits as a natural group.

Modern paleognathous birds include the ratites and tinamous. Ratites comprise one genus of ostrich (one species of *Struthio*, Struthionidae) from Africa and Asia, two genera of rheas (one species of *Rhea* and one species of *Pterocnemia*, Rheidae) from South America, one genus of cassowary (three species of *Casuarius*, Casuariidae) from New Guinea and northern Australia, one genus of emu (one living and one recently extinct species of *Dromaius*, Dromaiidae) from Australia, one genus of kiwi (three species of *Apteryx*, Apterygidae) from New Zealand, six recently extinct genera of moas (two species of *Anomalopteryx*, one or two species of *Megalapteryx*, two species of *Pachyornis*, two species of *Euryapteryx*, one species of *Emeus*, and three or four species of *Dinornis*, Dinornithidae) from New Zealand, and one recently extinct genus of elephantbird (four [?] species of *Aepyornis* and three species of *Mullerornis*, Aepyornithidae) from Madagascar. There are nine genera of living tinamous (five species of *Tinamus*, three species of *Nothocercus*, twenty-one species of *Crypturellus*, one species of *Rhynchotus*, seven species of *Nothoprocta*, five species of *Nothura*, one species of *Taoniscus*, two species of *Eudromia*, and two species of *Tinamotis*, Tinamidae), known from Central and South America.

Until recently, the fossil record of positively identifiable paleognathous birds was believed to begin rather abruptly in late Miocene and Pliocene deposits of South America, Asia, and Australia. This record has now been extended back to the late Paleocene by newly discovered *Diogenornis fragilis* Alvarenga, 1983 (Rheiformes: Opisthodactylidae) and species newly recognized as being paleognathous, including middle Eocene *Palaeotis weigelti* Lambrecht, 1928 (Struthioniformes: Struthionidae) (Houde and Haubold, 1987) and the Lithornithidae which are described herein. However, geologically older fossil birds have been described as being paleognathous. *Gobipteryx* (Enantiornithes), from the late Cretaceous of Mongolia was first described as paleognathous (Elżanowski, 1976) but was later recognized as distinct from the Palaeognathae (Elżanowski, 1977; Martin, 1983; Cracraft, 1986). *Gobipteryx* possesses some of the characters that collectively diagnose the paleognathous palate, but it exhibits a more typically reptilian quadrate bone. Based on postcranial characters, the Enantiornithes are not closely allied with either modern paleognathous or neognathous birds, regardless of their palatal morphology. *Hesperornis* (Hesperornithiformes), from the late Cretaceous of North America, was first likened to ratites by Marsh (1880) on the basis of postcranial characters and was later described as possessing a paleognathous palate by Gingerich (1973, 1976a). *Hesperornis* may, indeed, have possessed some of the characters associated with the paleognathous palatal complex but, from Gingerich's own reconstruction, it exhibited the most derived and bizarre jaw apparatus of any bird yet known. Brodkorb

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(1976), McDowell (1978), and Cracraft (1980) were clearly justified in removing *Hesperornis* from the ranks of the Palaeognathae. Their views are consistent with my observations that the pattern of microscopic vascular canals in the compacta of the tibiotarsus of *Hesperornis* is not like that of paleognathous birds (Houde, 1987a).

The Tertiary record of putatively paleognathous birds is reviewed by Olson (1985) and summarized in Table 1. (Fossils belonging to the new order Lithornithiformes are listed separately in Table 2.) Many of these taxa are true paleognathous birds, particularly members of extant families. Others are probably not paleognathous, however, and are assumed to be ratites for no other reason than that they are large flightless birds. Although *Remiornis* Lemoine, 1878 is typically grouped with the gruiform Gastornithidae, it is apparently a ratite (Martin, 1983) and is included here. The supposed eleutherornithid *Sauromis* Fischer, 1967 is not included here because it was recently discovered to be incorrectly based on a mammal bone (Haubold and Krumbiegel, 1984). In addition, fossil tracks and eggshells have been attributed to ratite birds. These allocations are too speculative to warrant recognition, although some are probably correct.

HISTORY OF THE CLASSIFICATION OF PALEOGNATHOUS BIRDS

The classification of paleognathous birds has a long but well-documented history. The most comprehensive treatments, among many, are those of Sharpe (1891), Dubois (1891), Shufeldt (1904), and Sibley and Ahlquist (1972). The last of these has been updated somewhat by Sibley and Ahlquist (1981) and Cracraft (1981). Only milestone works that contributed to the currently espoused classifications of paleognathous birds are reviewed here.

Merrem (1813) is often cited as the first to classify any of the paleognathous birds as a group but, in fact, Linnaeus (1758) treated ostriches, rheas, cassowaries, and emus as congeners in *Struthio*. Merrem coined the name "Ratitae," which refers to the absence of carina sterni in these birds. Although Merrem's Ratitae and Carinatae were only of ordinal rank, they formed the major dichotomy in his classification of modern birds and this popular tradition has lasted until now (Brodkorb, 1963; Houde and Olson, 1981). Only later were kiwis added to the Ratitae (Lesson, 1831).

Parker (1864) recognized the similarity of the "Struthious" and tinamou palates, although Huxley (1867) generally receives credit for this. Huxley (1867) was responsible for placing tinamous in the suborder Dromaeognathae, however, in allusion to their emu-like palate. He, nevertheless, retained them within the Carinatae of Merrem. Huxley, like many of his contemporaries (e.g., Seebohm, 1888; Fürbringer, 1888; Goodchild, 1891; and Gadow, 1892), felt that tinamous were most closely related to gallinaceous birds. Brodkorb (1963) later elevated Huxley's Dromaeognathae to the rank of infraclass but removed it from the Carinatae (which is also considered an infraclass by Brodkorb).

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TABLE 1. The Tertiary record of paleognathous and putatively paleognathous birds, exclusive of the Lithornithiformes. See Table 2 for the Lithornithiformes. Familial allocations follow doctrine and do not necessarily reflect my opinion. See text and Olson (1985) for comments.

PLIOCENE:
    TINAMIDAE:
        Eudromia olsoni Tambussi and Tonni, 1985; Argentina
        Nothura parvulus (Rovereto, 1914); Argentina
        Querandiornis romani Rusconi, 1958; Argentina
    STRUTHIONIDAE:
        Struthio asiaticus Milne-Edwards, 1871; India
        S. chersonensis (Brandt, 1873); Greece, Ukraine, Kazastan
        S. wimani Lowe, 1931; China, Mongolia
        S. bradydactylus Burchak-Abramovich, 1939; Odessa
    RHEIDAE:
        Heterorhea dabbenei Rovereto, 1914; Argentina
    DROMAIIDAE:
        Dromaius ocypus Miller, 1963; Australia
    DROMORNITHIDAE:
        Dromornis australis Owen, 1872; Australia
MIOCENE:
    TINAMIDAE:
        Eudromia sp. (Tambussi and Tonni, 1985)
    STRUTHIONIDAE:
        Struthio orlovi Kurochkin and Lungu, 1970; Moldavia
    OPISTHODACTYLIDAE:
        Opisthodactylus patagonicus Ameghino, 1891; Argentina
    DROMORNITHIDAE:
        Barawertornis tedfordi Rich, 1979; Australia
        Bullockornis planei Rich, 1979; Australia
        Dromornis stirtoni Rich, 1979; Australia
        Ilbandornis lawsoni Rich, 1979; Australia
        I. woodburnei Rich, 1979; Australia
OLIGOCENE:
    AEPYORNITHIDAE:
        Stromeria fajumensis Lambrecht, 1929; Egypt
        Eremopezus eocaenus Andrews, 1904; Egypt
    ELEUTHERORNITHIDAE:
        Proceriavis martini Harrison and Walker, 1979; England
EOCENE:
    ELEUTHERORNITHIDAE:
        Eleutherornis helveticus Schaub, 1940; Switzerland
    STRUTHIONIDAE:
        Palaeotis weigelti Lambrecht, 1928; Germany
PALEOCENE:
    OPISTHODACTYLIDAE:
        Diogenornis fragilis Alvarenga, 1983; Brazil
    FAMILY UNCERTAIN:
        Remiornis minor (Lemoine, 1878); France

TABLE 2.   Stratigraphic relationships of lithornithid taxa.

	NORTH AMERICA
EOCENE:	
Bridgerian	Lithornithidae, genus indet. (YPM 883)
Late Wasatchian	*Pseudocrypturus cercanaxius*
Early Wasatchian	*Paracathartes howardae* *Lithornis* cf. *nasi*
Middle Clarkforkian	*Lithornis promiscuus* *Lithornis plebius*
PALEOCENE:	
Early Tiffanian	*Lithornis celetius*
	EUROPE
EOCENE:	
?Ypresian, Plastic Clay	*Lithornis* cf. *nasi*
Ypresian, London Clay D-E	*Lithornis vulturinus* *Lithornis* cf. *plebius*
London Clay C	*Lithornis vulturinus*
London Clay B	*Lithornis hookeri*
London Clay A	*Lithornis nasi* cf. *Pseudocrypturus cercanaxius*
?Ypresian, Blackheath Beds	Lithornithidae, genus indet. (BMNH 14633)

Pycraft (1900) objected to Merrem's Ratitae-Carinatae dichotomy because the ratite condition of the sternum could be evolved secondarily by unrelated carinate birds. By this time characters from virtually all organ systems were already known to be uniquely shared by paleognathous birds, particularly the ratites. To distinguish the tinamous from other carinates and the ratites from secondarily flightless "carinates" (the term is used here in the taxonomic sense; Pycraft recognized that the flightless condition of ratites was also secondarily derived), Pycraft preferred to found his major subdivisions on the basis of palatal morphology. He considered the palatal condition of ratites and tinamous, indeed the birds themselves, to be primitive among

Aves, which is reflected in the etymology of his term Palaeognathae (Gr., old jaw). Thus, for the first time, tinamous were grouped with, not just near, the ratites.

Pycraft (1900) included seven orders (Casuarii, Struthiones, Rheae, Crypturi, Dinornithes, Aepyornithes, and Apteryges) in his "Grade" Palaeognathae. The Palaeognathae have most often been classed as a superorder, although Stresemann (1927–1934) treated them as a subclass and Cracraft (1981) reduced their rank to the ordinal level, changing the name accordingly to Palaeognathiformes. Cracraft's action followed from his conviction (following Bock, 1963) that paleognathous birds were monophyletic descendants of neognathous ancestors rather than primitive birds.

A quite different classification of paleognathous birds was introduced by Fürbringer (1888), who maintained that paleognathous birds are polyphyletic. He therefore classed them in four separate orders, one of which (Alectorornithes) even included gallinaceous birds. Fürbringer's precedent of treating paleognathous birds in separate orders, without a higher taxon in common to distinguish them from neognathous birds, has been followed by many other authors (McDowell, 1948; Mayr and Amadon, 1951; Wetmore, 1960; Storer, 1971) who agree that the ratites are a polyphyletic group.

Paleognathous birds have thus been placed together or apart at every taxonomic level from the genus to the subclass. Even recently there has been disagreement over whether they should be treated as one order (Cracraft, 1981), two orders within one superorder (Sibley and Ahlquist, 1981), two infraclasses (Brodkorb, 1963), or seven unrelated orders within the Neognathae (Storer, 1971). There is overwhelming evidence (discussed below) that paleognathous birds comprise a natural group, although not necessarily a strictly holophyletic one if fossil forms are included, and should be grouped together. Although the taxonomic rank assigned them is arbitrary and not of primary importance, paleognathous birds are sufficiently distinct from all other birds, from their gross anatomy and behavior right down to their molecular constituents, that they probably deserve to be separated from all other modern birds at the highest taxonomic level within Neornithes. Accordingly, microcomplement fixation (Prager, et al., 1976; Prager and Wilson, 1980) and protein sequencing studies (Stapel, et al., 1984) show the paleognath-neognath divergence to be the earliest in the history of birds.

PHYLOGENETIC HYPOTHESES ABOUT THE RELATIONSHIPS OF PALEOGNATHOUS BIRDS

The relationships of paleognathous birds has been one of the most debated questions in avian systematics over the last century (Bock, 1963; Cracraft, 1974; Houde and Olson, 1981; Sibley and Ahlquist, 1981; Olson, 1985). Here I provide justification for treating paleognathous birds as a natural group in response to the considerable differences of opinion about paleognath relationships that persist in the literature.

Paleognathous birds have been described as polyphyletic, monophyletic,

and paraphyletic and as being primitive, specialized, and neotenic. Most of the literature on this problem has been summarized by Sibley and Frelin (1972) and Sibley and Ahlquist (1972, 1981). Until now the fossil record has been insufficient to provide direct evidence of paleognath relationships. Consequently, systematists have had to rely almost exclusively on neontological studies in order to reconstruct the phylogeny.

Many early authors and some contemporary researchers (Fürbringer, 1888; Harrison, 1915; Stresemann, 1927–1934; McDowell, 1948; Mayr and Amadon, 1951; Cameron, 1952; Wetmore, 1960; Osuga and Feeney, 1967; Storer, 1971; Mayr, 1974; Feduccia, 1980; Olson, 1985) consider paleognathous birds to be a polyphyletic assemblage of convergent lineages. These conclusions are based on their own studies, and those of others, of comparative osteology, myology, pterylography, reproductive systems, parasitology, egg white proteins, and (neognath) paleontology. In general, these authors are more impressed by the differences than by the similarities among paleognathous birds. Others presented evidence based on comparative studies of anatomy and development (de Beer, 1956), embryology (Webb, 1957), osteology (Verheyen, 1960a), cephalic anatomy (Hofer, 1950; Stark, 1955; Lang, 1956; Saiff, 1982), cranial kinesis (Simonetta, 1960; Elźanowski, 1977), eggshell histology (Tyler, 1956; Tyler and Simkiss, 1959), carotid arteries (Glenny, 1965), and proteins (Sibley and Frelin, 1972; Sibley and Ahlquist, 1972; Krampitz, et al., 1974) that either suggested or could be construed to imply separate origins of at least some ratites, especially kiwis.

It has frequently been contended that tinamous are related to (although not necessarily *most* closely related to) the Galliformes (Seebohm, 1888; Goodchild, 1891; Beddard, 1898, 1911; Clark, 1901; Chandler, 1916; Clay, 1950, 1957; Dubinin, 1958; Verheyen, 1960b–d, 1961; Banks, 1970; Gysels, 1970; McFarlane, 1971; Sibley and Frelin, 1972; Sibley and Ahlquist, 1972) because of similarities in their osteology, myology, intestinal morphology, pterylography, molt, spermatozoa, and protein electrophoretic patterns. Tinamous may, in fact, represent a phylogenetic "link" between paleognathous and neognathous birds. Most ornithologists accept, whether correctly or not, that the relationship between tinamous and gallinaceous birds is probably real, although not yet rigorously documented.

A growing body of authors has rallied either wholly or partially in support of the hypothesis of paleognath, and particularly ratite, monophyly or have provided evidence that has been cited by other authors to support this hypothesis. This evidence is, overall, more diverse than that which has been used to support the model of paleognath polyphyly. Similarities have been reported in paleognath vertebrae (Mivart, 1874, 1877), palates (Hofer, 1945, 1955; Bock, 1963, 1964), eustachian tubes (Hopkins, 1906), middle ear (Saiff, 1983), parasites (Kellogg, 1913), coelomic cavities (Duncker, 1979), osteology (Cracraft, 1974, 1986), jaw adductors (Hofer, 1950), behavior (Meise, 1963), carotid arteries (Glenny, 1965; Baumel, 1968), rhamphothecal grooves (Parkes and Clark, 1966), plumage as chicks (Pycraft, 1900; Jehl, 1971), pterylography (Chandler, 1916; Parker, 1864), spermatozoa (McFarlane,

1971), proteins (Sibley, 1960; Miller and Feeney, 1964; Wilson, et al., 1964; Kaplan, 1965; Fitch and Margoliash, 1967; Prager, et al., 1976; Osuga and Feeney, 1968; Feeney and Alison, 1969; Gysels, 1970; Sibley and Ahlquist, 1972; Sibley and Frelin, 1972; Krampitz, et al., 1974; Ho, et al., 1976; Prager and Wilson, 1980; Stapel, et al., 1984), and DNA (de Boer, 1980; Sibley and Ahlquist, 1981, 1985). Many of these authors described similarities among only some paleognathous birds, though, and also found differences between others.

In addition to lending credibility to the hypothesis of paleognath monophyly, several authors have either maintained, or provided evidence that supports the hypothesis, that paleognathous birds are phylogenetically primitive, or at least morphologically archaic, within Aves or that they had a separate ancestry from coelurosaurian reptiles than did neognathous birds. Their work includes studies of the palate (Huxley, 1867; Pycraft, 1900; Simonetta, 1960; McDowell, 1978), pterygoideus muscles (Hofer, 1950), pectoral and pelvic girdles (Marsh, 1880; Parker, 1891; Lowe, 1928, 1935; Friant, 1945a,b, 1946, 1959; Holmgren, 1955; Glutz von Blotzheim, 1958; Feduccia, 1986), bone histology (Amprino and Godina, 1944; Zavattari and Cellini, 1956), tarsal osteology (McGowan, 1984), wing myology (McGowan, 1982), sinus venosus of the heart (Adams, 1937–kiwis only), gonads (Kinsky, 1971–kiwis only; Meier, 1979), bursa of Fabricius (Berens von Rautenfeld and Budras, 1982), cortical neuroanatomy (Craige, 1935a,b, 1940a,b; Pearson, 1972), proteins (Wilson, et al., 1964; Kaplan, 1965; Prager, et al., 1976; Prager and Wilson, 1980; Stapel, et al., 1984), and karyology (Takagi, et al., 1972; Takagi and Sasaki, 1974).

At present the most popular model of the origins of paleognathous birds is that they are holophyletic (Bock, 1963, 1964; Cracraft, 1974), having evolved from neognathous ancestors. Reports that paleognathous birds are neotenic or secondarily flightless (McDowell, 1948; de Beer, 1956, 1964; Webb, 1957; Jollie, 1958; Tyler and Simkiss, 1959; Feduccia, 1980) and, therefore, "derived" have been cited (e.g., Cracraft, 1974) in support of the hypothesis of paleognath holophyly. Some of the fossil paleognathous birds described herein were excellent fliers, thus good flight should not be thought of as a trait unique to neognathous birds. The ancestry of paleognathous birds need not be sought among neognaths using flight capability as a criterion.

Some authors (Gingerich, 1976a; Houde and Olson, 1981) have suggested, alternatively, that paleognathous birds, *including* extinct forms, could be a paraphyletic group that was ancestral to neognathous birds. This hypothesis gains support from the studies cited above that suggest paleognathous birds constitute a primitive or archaic group of birds, and it is consistent with most studies that advocate a monophyletic origin of paleognathous birds. While paleognathous birds may indeed share homologous characters with each other that are absent in other birds, this may be only because such characters were secondarily lost or modified by the early common ancestors of neognaths after their divergence from paleognaths.

A still newer interpretation (Cracraft, 1986; see, also, Houde, 1987a) is that

the characters that have traditionally been used to unite paleognathous birds are primitive, but both paleognathous and neognathous birds are holophyletic groups that evolved from the same ancestor that was neither paleognathous or neognathous, itself, by current definitions.

DNA hybridization studies (Sibley and Ahlquist, 1981, 1985) establish that extant ratite birds comprise a monophyletic group, relative to tinamous. Although the evidence is as yet unpublished, these investigators support the monophyly of all extant paleognathous birds (poster, XIXth International Ornithological Congress, 1986, Ottawa). Their studies do not, however, settle the questions of whether paleognathous birds are holophyletic or paraphyletic, the correct polarities of morphological characters they exhibit, where and when they arose, or how many times flightlessness was evolved by ratites.

MATERIALS AND METHODS

The procedure for this research has seven parts: (1) field collecting of fossils, (2) removal of the fossils from rock, (3) preparation of ground "thin sections" of bones and eggshell for light microscopy, (4) museum study, (5) identification, definition, measurement, and naming of taxa, (6) phylogenetic analysis, and (7) interpretation of functional anatomy and paleoecology. Paleontological materials and methods are generally so well understood that detailed description of them is usually unwarranted. However, some of my methods are rather unorthodox and deserve special attention.

FIELD COLLECTING

Field collecting was undertaken for parts of five summers in Tiffanian (late Paleocene) sediments of the Fort Union Formation in the Western Crazy Mountain Basin of Montana and in Clarkforkian and Wasatchian (late Paleocene to early Eocene) sediments of the Willwood Formation in the Bighorn Basin of Wyoming. Rather than collecting fossils from the erosional surface of mudstones, as is the common practice in these areas, fossils were collected exclusively from discrete calcareous nodules. In Montana nodules were collected by digging a quarry (see Gingerich, Houde, and Krause, 1983). In Wyoming, however, where sediments are better exposed, large tracts of land were surveyed and nodules were collected only from or near the surface.

My success in obtaining the North American fossil birds reported on here is directly due to the practice of sampling calcareous nodules. The nodules are easily located and commonly contain lithornithid bones and eggshell, as well as many other small vertebrate remains. I donated the non-avian remains that I collected to the Museum of Paleontology, University of Michigan, where they are being studied separately (e.g., Rose and Gingerich, 1987). Specimens found in nodules are better preserved and better associated than those collected from mudstones. The difference between collecting from mudstone deposits and from calcareous nodules is well exemplified by the study of Winkler (1981), who showed that, at a particular study site, screen washing mudstones yielded more small vertebrates than surface collecting. However, he found no birds by either method, while I recovered in excess of 100 bird bones from a single nodule, plainly exposed at Winkler's study site.

The mode of formation of the nodules remains enigmatic, but some generalizations can be made. Often many entire carcasses, gastropods, and plant debris were concentrated in what was probably a small wet depression with discrete boundaries. In most instances burrowing organisms disarticulated the skeletons, but all the bones of an individual organism usually remained within the confines of the nodule. Calcareous accretion presuma-

bly occurred postdepositionally, usually before subsidence was substantial enough to cause dewatering and diagenesis.

REMOVAL OF FOSSILS FROM ROCK

Fossiliferous calcareous nodules are dissociated in baths of dilute (7–12%) acetic acid. The fossil bones are etched less rapidly than the rock due to their crystalline structure and presumably phosphatic composition. After each 24- to 48-hour period of etching, the nodules are removed from the acid, rinsed in fresh water, and allowed to dry. Newly exposed portions of bones are then coated with a solution of polyvinyl acetate in acetone to protect them from the acid. Only one or two millimeters of rock are removed with each etching and the process is continued for months or years for individual nodules. Large nodules (up to 250 lbs.) that can not be easily raised in and out of the acid baths are treated somewhat differently. These are first coated on all but one side with several layers of latex rubber in order to seal them and also to act as a separator between fossils and polyester, which is applied to the rock next. Polyester laminating resin and fiberglass cloth are layered onto the rock, leaving one side uncoated, and built up to form walls around the uncoated surface of the rock. Acid is then poured directly on top of the exposed portion of the nodule, with the fiberglass forming a container for the acid bath.

PREPARATION OF GROUND LAPIDARY THIN SECTIONS

Transverse lapidary "thin sections" of the diaphysis and/or distal meta-physis were made from tibiotarsi of *Lithornis celetius* (USNM 290554) and *Paracathartes howardae* (USNM 361407), as well as from other paleogna-thous and neognathous birds, for comparison (see Houde, 1987a). I also made thin sections of the tibiotarsus of *Hesperornis* sp. (YPM PU 22443) and *Eobucco* sp. (USNM 336571), and of the tibiae of two unidentified fossil mammals (USNM 336572, 336573) that were associated with *Paracathartes howardae* (USNM 361407), to serve as controls for the effects of fossilization. These thin sections were interpreted with the aid of the description of the bone histology of paleognathous and neognathous birds set forth by Amprino and Godina (1944) and Zavattari and Cellini (1956).

Lapidary thin sections were also made from the eggshells of (1) *Lithornis celetius* (PU 16961), (2) cf. *Paracathartes howardae* (USNM 336575), (3) *Nothoprocta pentlandii* (USNM 47310, 47311), (4) *Apteryx australis* (USNM 46503), (5) *Rhea americana* (USNM 15850), (6) *Crax rubra* (USNM 18854), and (7) *Gallus gallus* (store-bought). Numbers 1 and 2 are lithorni-thids, 3 is a tinamou, 4 and 5 are ratites, and 6 and 7 are neognathous outgroups. Thin sections of eggshells were interpreted with the aid of the description of the eggshell histology of paleognathous birds set forth by Tyler and Simkiss (1959).

MATERIALS AND METHODS

Care was taken in the preparation of lapidary thin sections to insure that the plane of the cut was consistently transverse across tibiotarsi and radial across eggshells. The thicknesses of the specimens were not measured. The thickness of sections was governed by light transmittance and resolution. Cover-slips were used and glued to the specimens with Epon epoxy.

Specimens were examined with bright field microscopy. Figures of thin sections in this paper were enlarged by different amounts from the original negative size so that photographs within each figure are of comparable size.

MUSEUM STUDY[1]

Museum study involved examination of fossil specimens at the following museums: Museum of Comparative Zoology, Harvard University; Museum of Paleontology, University of Michigan; Peabody Museum of Natural History, Yale University; Museum of Natural History, Princeton University; Museum of Natural History, University of Kansas; American Museum of Natural History, New York; Brodkorb Collection, Gainesville, Florida; Museum of Geology, University of Wyoming; Geological Museum, University of Colorado; National Museum of Natural History, Washington; Field Museum of Natural History, Chicago; Carnegie Museum of Natural History, Pittsburgh; British Museum (Natural History), London and Tring; the private collection of Michael C. S. Daniels, Essex, England; Geologisk Museum, University of Copenhagen; Geiseltalmuseum, Halle a. Saale; Hessisches Landesmuseum, Darmstadt; Senckenbergmuseum, Frankfurt am Main; Museum National d'Histoire Naturelle, Paris; and Universite Claude Bernard (Lyon I), France. I also examined relevant fossil material brought by visiting scientists to the Smithsonian Institution from Moscow and Rio de Janeiro.

Initial museum study was chiefly concerned with the determination of the nearest relatives of lithornithids. To this end representatives of all non-passerine families of birds were examined in the systematic skeletal collections of the American Museum of Natural History, the National Museum of Natural History, and the Museum of Natural History, Princeton University.

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[1]Abbreviations employed in the text are: **AMNH** Department of Vertebrate Paleontology and Department of Ornithology, American Museum of Natural History; **BMNH** Department of Palaeontology, British Museum (Natural History); **HLMD** Hessisches Landesmuseum, Darmstadt, Federal Republic of Germany; **LACM** Natural History Museum of Los Angeles County; **MMH.V.P.** Geologisk Museum, University of Copenhagen; **PA** Department of Vertebrate Paleontology, Field Museum of Natural History; **PU** Princeton University Collection (now at Peabody Museum of Natural History, Yale University); **ROM** Royal Ontario Museum; **UK** Museum of Natural History, University of Kansas; **UM** Museum of Paleontology, University of Michigan; **USNM** National Museum of Natural History, Smithsonian Institution; **WN** private collection of Michael C. S. Daniels, Essex, England; **YPM** Peabody Museum of Natural History, Yale University.

MATERIALS AND METHODS

To assess intraspecific polymorphism in neospecies of tinamous as a model for interpretation of fossils, I studied specimens of *Rhynchotus rufescens*, *Nothura maculosa*, and *Eudromia elegans* in the U.S. National Museum of Natural History, and borrowed all the specimens of these three species from the American Museum of Natural History, Carnegie Museum of Natural History, British Museum (Natural History), Natural History Museum of Los Angeles County, Peabody Museum of Natural History, University of Michigan, University of South Florida, Tampa, Natural History Museum, San Diego Society of Natural History, Uppsala University Institute of Zoology, University of Kansas Museum of Natural History, Museum of Comparative Zoology, and Royal Ontario Museum.

NOMENCLATURE

The anatomical terminology in this paper generally follows Baumel (1979), but sometimes Howard (1929), depending upon general usage. I have used the universally understood terminology of human anatomy where homology is unquestionable. A few characters that are found only in paleognathous or Mesozoic birds are not named by these authors. In these instances I have cited the original papers in which these characters were named.

MENSURATION

All measurements of specimens are given in tables, arranged according to elements, not taxa. Measurements are given in millimeters unless specifically stated otherwise. In the tables measurements are always exact and are never estimated, except in Table 4 where the symbol $\sim$ indicates that the bilateral width was estimated by doubling a measurement taken from only one side. Elsewhere the character $\sim$ preceding a measurement means that the measurement is probably not accurate because of diagenetic damage to the specimen or unremoved matrix. Except in the case of holotype specimens, if a measurement seemed to be imprecise by more than plus or minus one millimeter because of crushing or unremoved matrix, then the measurement was not given at all. The character $>$ preceding a measurement indicates that the measurement is smaller than its true value because a piece of the bone is broken or missing. In most cases only one millimeter or less of bone is probably missing. The character $<$ preceding a measurement indicates that the measurement is obviously larger than its true value because of diagenetic distortion. Measurements preceded by the character $>>$ are more than five millimeters shorter than they would be in an intact specimen.

PHYLOGENETIC ANALYSIS

Phylogenetic analysis of the Lithornithidae begins with the identification of species units. This is an arbitrary process that depends heavily on one's

perception of the degrees of individual variation in modern birds. I used large samples of modern tinamou skeletons as a model to assess intraspecific variability in the fossils. In the interest of conservatism, specimens are lumped as much as possible in this paper and many small individual differences are overlooked. Particularly problematic specimens (often fragmentary fossils from somewhat different ages and collecting localities than more complete specimens) are listed separately; only clearly defined species are described.

Anatomical characters, whether gross or microscopic, are evaluated cladistically on the basis of their distributional patterns in ingroups and outgroups. Ingroups are sister taxa, or members of the same monophyletic clade, whereas outgroups are not members of the same clade. A monophyletic clade is a group of organisms of common ancestry. A holophyletic clade is a self-inclusive monophyletic clade that consists of all of the evolutionary derivatives of its common ancestor. A paraphyletic clade is a monophyletic clade that does not include all of its evolutionary derivatives. A character shared by two or more taxa is determined to be synapomorphous, symplesiomorphous, or homoplasious on the basis of the degree of similarity of the structure and the diversity of the taxa in which it is exhibited. Synapomorphous and symplesiomorphous characters are homologous, but homoplasious characters are nonhomologous unless convergent by evolutionary reversal. A synapomorphous, or shared derived, character is an evolutionary novelty that is present in two or more taxa due to recent common ancestry. It uniquely defines all organisms that possess it as members of a monophyletic clade. Symplesiomorphous, or shared primitive, characters are inherited from a distant common ancestor by organisms that are not all members of a holophyletic clade. Cladograms that incorporate this information attempt to reflect, or reasonably approximate, evolutionary histories, if the characters examined are correctly identified as being synapomorphous, symplesiomorphous, or homoplasious.

Throughout this paper, the use of the phrase "natural group" is broader than its strictest cladistic meaning, in which the organisms described are members of a holophyletic clade. Instead, I use "natural group" in reference to any group of organisms that might be considered to have been monophyletic at some time during their evolution. By this broad definition, paraphyletic groups that were ancestral to other lineages are considered to be natural groups because they share morphological characters (either primitive or derived) as the result of common ancestry. This is an attempt on my part to do away with the dichotomous treatment of extant and extinct organisms. Thus, the fossil Lithornithidae described herein are considered to be a natural group, regardless of their possibly paraphyletic relationship, because they comprise a morphologically uniform and coherent assemblage, the members of which share a common ancestry.

With an *a priori* assumption that paleognathous birds constitute a natural group, the polarities of characters help us to choose the most likely phylogenetic hypothesis, given several alternative hypotheses such as the

examples shown in Figure 1. The first of these alternative hypotheses is that paleognaths are holophyletic (Figs. 1a and 1c). The second is that they are paraphyletic (Figs. 1b and 1d). If lithornithids are the sister group either of extant paleognathous or of neognathous birds (Figs. 1c and 1d) then the questions of the relationships of paleognathous and neognathous birds and the interordinal relationships of the Lithornithidae are synonymous problems.

The four cladograms in Figure 1 do not account for all the possible phylogenetic reconstructions of paleognathous and neognathous birds, but instead represent the simplest forms of dichotomous trees that I believe most likely reflect actual evolutionary pathways. I have not restricted my examination to the four hypotheses shown in Figure 1 but I have not considered all the possible branching patterns that could possibly be drawn. First, I have assumed that both paleognathous and neognathous birds are natural groups, whether holophyletic or paraphyletic, and I have not considered cladograms that present these taxa as polyphyletic. Second, I have not seriously examined cladograms that place ratites intermediate between neognathous and other paleognathous birds. Furthermore, the genealogical relationships of Figures 1a and 1c could be correct while, at the same time,
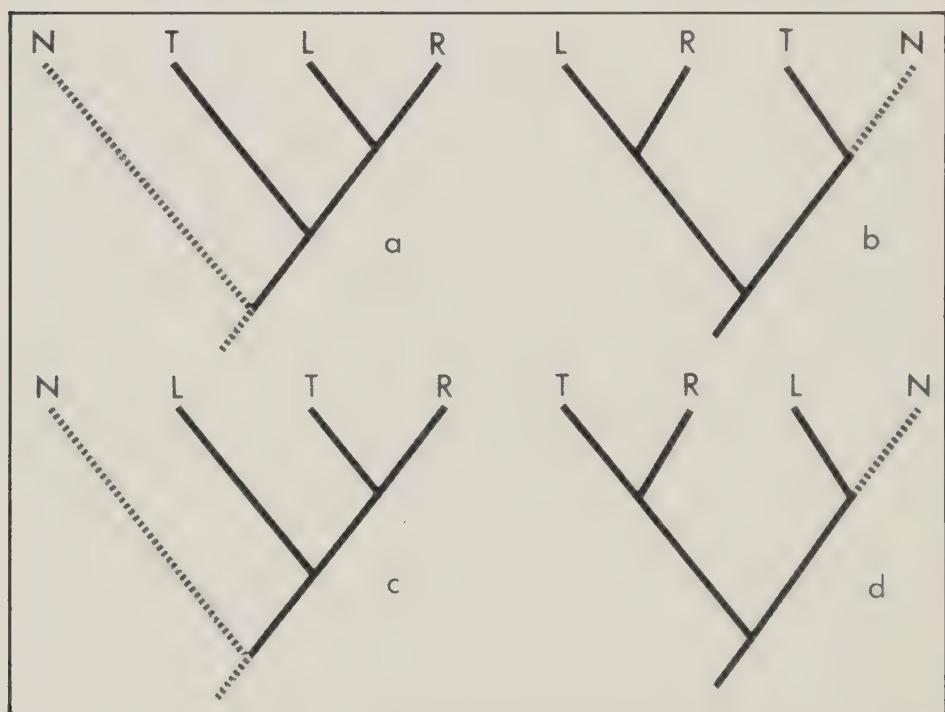
Fig. 1. Some hypothetical phylogenies of paleognathous and neognathous birds of unequal rank. See text (above) for details. Broken line = neognathous character state; solid line = paleognathous character state. Abbreviations: L—Lithornithiformes, N—neognathous birds, T—Tinamiformes, R—ratites.

the character state polarity I have indicated was not (compare Figs. 1a and 40b). The detailed cladograms figured at the end of this paper, in fact, represent the Lithornithidae as a paraphyletic family and are not directly comparable to those of Figure 1.

I make no pretense that these phylogenetic reconstructions represent anything more than working hypotheses. There are simply too few primitive outgroups among birds that can be used to establish character polarities in paleognathous birds with certainty. As new primitive outgroups are discovered, new analyses will be warranted.

EVALUATION OF ADDITIONAL HYPOTHESES

The new paleontological data presented herein has the potential to shed light on two hypotheses, in addition to the phylogenetic hypotheses introduced above. These are Bock's (1963, 1964) hypothesis of paleognath holophyly and Cracraft's (1973, 1974) hypothesis of vicariance biogeography to explain ratite origins and distribution. Although these hypotheses are largely phylogenetic, they are discussed separately because of their wide acceptance.

3
SYSTEMATIC PALEONTOLOGY

CLASS **AVES** Linnaeus, 1758

SUBCLASS **NEORNITHES** Gadow, 1893

SUPERORDER **PALAEOGNATHAE** Pycraft, 1900

LITHORNITHIFORMES, new order

DIAGNOSIS

The rhynchokinetic skull, paleognathous palate and carinate sternum separate members of this order from all other sufficiently known orders of birds except Tinamiformes. The Lithornithiformes differ from Tinamiformes as follows: (1) the pterygoid is broad and (2) possesses a pterygoid fossa; (3) the occipital condyle is large; (4) the sternum lacks deep notches in its posterior margin; (5) the coracoid has a flat and broad sternal extremity and (6) a flange-like furcular attachment; (7) the scapula has a long and pointed acromion; (8) the humerus has a large pectoral crest and (9) a round ventral tubercle (internal tuberosity); (10) the ischium tapers to a point caudally; (11) the femur has a low trochanteric crest and (12) a small but wide medial condyle; (13) the tarsometatarsus has a knob-like hypotarsus, (14) a large interosseous canal, and (15) a deep impression of the extensor brevis digiti IV muscle.

LITHORNITHIDAE, new family

TYPE GENUS
Lithornis Owen.

INCLUDED GENERA
Lithornis Owen, *Paracathartes* Harrison, and *Pseudocrypturus* n.g.

DIAGNOSIS
As for the order.

DESCRIPTION*

The following applies to all members of the family to the extent that they are presently known. Parts of this description are based on only a few specimens; some characteristics may eventually be shown not to be present in all members of the family.

* The Figures and Tables for Chapter 3 appear at the end of the chapter, on pages 44 through 105.

SYSTEMATIC PALEONTOLOGY

SKELETON

Skull (Figs. 2–8; Table 3).—Meets all the criteria collectively accepted as diagnostic of the paleognathous palate and rynchokinetic skull: the vomer is long, extending from the premaxillae to the pterygoids; the palatines are continuous with the pterygoids and no suture is visible between them; basipterygoid processes are present and articulate extensively with the caudal extremity of the pterygoids; the pterygo-quadrate articulation is extensive and complex and includes a large portion of the orbital process of the quadrate, the articular surface of the pterygoid being the shape of a bent hourglass and the corresponding surface of the quadrate being saddle-shaped; the zygomatic process is large and closely applied to the lateral surface of the quadrate; the lateral nasal bar is unfused ventrally; and the nasal septum is very extensive and continuous with the orbital septum.

Similar to tinamous with respect to: the straight and fragile bill; the acute angle formed by the posterior margin of the nares; the broad prefrontals; the moderately narrow supraorbital region; details of the postorbital process, zygomatic process, and tympanic cavity; the palatal bone with caudal process (*Pseudocrypturus* only); and the presence of Müller's (1963) "foramen jugulare spurium" or Whetstone's (1983) apparently equivalent "post-temporal fossa." The basicranium is like *Eudromia* and its allies, not *Rhynchotus* with its parabasal tubercles (see Elźanowski, 1987: fig. 15, not fig. 3). The lateral nasal bar meets but does not fuse with what seems to be the palatine process of the maxilla, and is narrow dorsally, broader ventrally. The lateral nasal bar varies considerably in thickness in different genera. In *Lithornis* it is similar to that of tinamous but in *Pseudocrypturus* it is similar to some kiwis (*Apteryx australis* and *A. mantelli*, not *A. oweni*).

The skull differs from that of tinamous and is more similar to that of kiwis with respect to: the greater length of the bill; the extensive nasal septum; configuration and robust structure of the palatal complex, particularly the broad pterygoid and presence of a large pterygoid fossa and absence of caudal palatal process in *Lithornis* and *Paracathartes*; the lack of fusion of the vomer and premaxillae in *Lithornis* and *Paracathartes*; the large occipital condyle; and the shallow depression in and the broadness of the fronto-nasal region of the bill. The lateral edge of the dorsal nasal bar curves ventrally at the base of the bill to form an osseous lateral wall of the nasal cavity. There is extensive ossification of parasagittal septa within the nasal cavity but these septa do not resemble those of kiwis. The fronto-parietal articulation remains unfused, the suture being smooth and unconvoluted apparently throughout ontogeny, as also appears to be true of at least two Mesozoic birds, *Archaeopteryx* and *Enaliornis* (Whetstone, 1983). The premaxillae are perforated by many large nerve endings.

Quadrate (Fig. 8).—The otic process lacks distinct prootic and squamosal condyles and, in detail, resembles that of tinamous in its medial curvature. The rest of the quadrate more closely resembles that of kiwis: there is no distinction between lateral and caudal condyles of the mandibular process; a buttress for the quadratojugal lies anterior to the lateral mandibular condyle

(also present in some tinamous); and the articulation of the pterygoid includes a large portion of the orbital process and incorporates no condyle. The orbital process is short, unlike other paleognathous birds. The mandibular condyle is flush with the lateral surface of the otic process.

Mandible (Figs. 7 and 8).—The splenial is unfused, long, thin, and extends to or near the mandibular symphysis as in all modern paleognathous birds and many reptiles. The ventral surface of the dentary particularly resembles that of kiwis, as it is perforated by many large foveae for nerve corpuscles (rostral rami of the mandibular nerve) and exhibits bilateral grooves in addition to the rhamphothecal grooves of Parkes and Clark (1966), which together form a "W"-shaped pattern. The articular is unique among birds and is approached only by kiwis in the following characters: the retroarticular process is pronounced, forms a "V"-shaped notch with the anterior portion of the lateral condyle, and actually forms a part of the mandibular-quadrate articulation.

Hyoid.—The basihyal is long and narrow.

Cervical Vertebrae (Table 4).—There are a total of 15 cervical vertebrae, based on *Pseudocrypturus;* the neural arches are tall and vault-shaped; the bodies are narrow; the diapophyses are very wide; and most vertebrae exhibit deep pits posteromedial to the anterior zygapophyses. Generally, the cervical vertebrae are intermediate between those of tinamous and cassowaries.

Thoracic Vertebrae (Table 4).—There are a total of eight thoracic vertebrae, based on *Pseudocrypturus;* there is a large pneumatic foramen on the lateral surface of each body. There is no notarium.

Caudal Vertebrae (Table 4).—Free caudal vertebrae lack well developed lateral processes.

Pygostyle (Table 4).—Is small and rudimentary; segmentation is visible in some specimens. Most species exhibit a pronounced ventral process that is not fused to the centrum anteriorly.

Sternum (Figs. 9–11; Table 5).—The width is equal to approximately one-half the length; the sternocoracoid process is short or directed postero-laterally; there are very few costal processes; the coracoidal sulci cross at the midline; the manubrium is prominent, slender, and unbranched; and the posterior margin is truncate and unnotched.

Furcula (Table 6).—There is no hypocleideum and the omal (dorsal) extremity lacks an articular facet.

Coracoid (Figs. 12 and 13; Tables 7 and 8).—The sternal extremity is dorsoventrally thin but mediolaterally very broad; the shaft is often very narrow; the sternal facet is indistinct; the impression of the acrocoracohumeral ligament is often large and deep; the scapular cotyla is large and deep; there is no facet for the articulation of the furcula; there is a conspicuous intermuscular line near the lateral margin of its ventral aspect; and there are one or more pneumatic foramina facing the triosseal canal.

Scapula (Fig. 14; Table 9).—The acromion is long and pointed, unlike any other known bird except *Ambiortus* (Ambiortiformes), and is perforated by a pneumatic foramen that faces the triosseal canal. The glenoid facet is

narrow and separated from the acromion by a deep notch anteriorly. The body of the scapula is long, straight, and narrow in small species, but broader and more curved in large species.

Humerus (Figs. 15–17; Tables 10–11).—Is pneumatic; its shaft is strongly curved; the caput is narrow; the bicipital crest is knob-like as in tinamous, but more like touracos (Musophagidae) and trumpeters (Psophiidae); the pectoral crest is long, pronounced, and arcuate as in many raptorial birds (Falconiformes and Strigiformes); the coracobrachial region is shallow; the ventral tubercle (internal tuberosity) is positioned closer to the shaft (more dorsally) than in modern birds, in which the tubercle is more closely associated with the bicipital crest, ventrally; the insertion of the latissimus dorsi muscle is positioned on the dorsal side of the shaft; the tricipital grooves are indistinct, as in tinamous; the medial epicondyle is moderately long and bulbous; the capitulum (doral condyle) is inflated, not narrow proximally; and the brachial depression is very shallow.

Radius (Fig. 18, Tables 12 and 13).—Is shorter than the humerus; the distal condyle is broad; and muscle scars extend virtually the entire length of the shaft.

Ulna (Fig. 19; Tables 14 and 15).—Is shorter than the humerus; there is a tendency for flattening of the shaft and distal condyles.

Carpometacarpus (Fig. 20; Tables 16 and 17).—The minor metacarpal is straight, not bowed, and lies considerably more ventrally than the major metacarpal (this is especially apparent in distal view); there is no intermetacarpal process. The carpometacarpus resembles those of megapodes (Megapodidae) and tinamous but is relatively longer and more slender.

Pelvis (Figs. 21 and 22; Table 18).—The width is equal to or less than one third of the length; the preacetabular portion of the ilium is oriented close to the dorsoventral plane and is variable in its dorsoventral height, being similar to tinamous in small specimens but similar to trumpeters (Psophiidae) in large specimens; the pectineal process is well developed but not long; the supra-acetabular region is tall and broad, as in trumpeters and somewhat like cassowaries; the anterior iliac crest is pronounced, especially dorsal to the acetabulum; the dorsolateral (postacetabular) iliac crest is very broad relative to the very medially positioned crest for the attachment of the ilioischiadic membrane (located on ventral or internal aspect of ilium); the ilium and ischium are unfused caudally (although in one specimen they may have met); the crests on the ilium and ischium that indicate the attachment of the ilioschiadic membrane are not present on the anterior one-half of the ilioischiadic foramen so it appears as though the condition of the foramen was more like that of neognathous birds; and the caudal extremity of the ischium is variable, being tapered to a point in some species, as in adult neognathous birds, but being considerably more truncate in other species, as in immature neognathous birds, tinamous, kiwis, and moas.

Femur (Figs. 23 and 24; Tables 19 and 20).—Moderately long and curved; superficially similar to that of limpkins (Aramidae); the trochanteric crest is low; the insertion of the iliotrochanteris caudalis muscle is large, deep,

centrally located, usually oval, and in most species resembles that of kiwis and hoatzins (Opisthocomidae); the medial condyle is small in medial view and set well apart from the tibiofibular crest by a deep groove as in the tinamous and kiwis.

Tibiotarsus (Fig. 25; Tables 21 and 22).—The cnemial crest is low and resembles that of the tinamous of open country, e.g. *Rhynchotus;* the lateral crest is more pronounced than the anterior crest; the tendinal groove is present and positioned medially on the anterior face of the shaft, but the osseous tendinal bridge is absent and thus resembles cassowaries; there is a prominent flattened process located centrally in the supracondylar region; and the variable configuration of the condyles is like tinamous, kiwis, or moas.

Tarsometatarsus (Figs. 26 and 27; Tables 24 and 25).—A lip projects from the posterolateral margin of the lateral cotyla to buttress a free ossicle of the intertarsal joint as in tinamous and kiwis and apparently all ratites; the intercotylar eminence is usually small but always distinct and spherical in anterior view; the hypotarsus is knob-like and lacks perforations; the infra-cotylar region is deeply excavated and this concavity is continuous distally with the distinctly sculptured origin of the extensor brevis digiti IV muscle and the large interosseous canal; the middle trochlea is procumbent, is usually square in distal view and often asymmetrical in anterior view, and the inner and outer trochleae are unequally elevated and considerably so.

Digits (Table 26).—Moderately robust, like those of the chicken (*Gallus*); the distal phalanges are hooked and narrow; there is a tendency for reduction of the hallux in some species.

BONE HISTOLOGY

In the compacta of the tibiotarsus of one specimen of *Lithornis* (USNM 290554), microscopic vascular canals are predominantly oriented parallel to the longitudinal axis of the bone, as in tinamous (Figs. 28–30). In the tibiotarsus of one specimen of *Paracathartes* (USNM 361407), vascular canals are arranged in concentric rows around the long axis of the bone, with either some fusion and anastomosing of adjacent canals or some canals that course in concentric circles in the transverse plane, as described for ratites by Amprina and Godina (1944), Zavattari and Cellini (1956), and Houde (1987a).

EGGS

Poles symmetrical (Fig. 31); external surface glossy with large widely spaced pores visible to the naked eye; pores simple and conical in radial thin section; eggshell thick with presumed "cuticular layer of true shell," like that described by Tyler and Simkiss (1959).

BEHAVIOR

Probably a mating system of simultaneous polygyny and sequential polyandry as in tinamous and some ratites (Meise, 1963; see p. 118). Some

species (genus *Lithornis*) probably were excellent sustained fliers, others were poorer fliers (genera *Paracathartes* and *Pseudocrypturus*). They probably foraged for insects, berries, and seeds by rooting through ground litter or probing with sensitive bill.

HABITAT

Temperate and subtropical seasonal forests near water in late Paleocene to middle Eocene of North America and Europe (see p. 107).

DISTRIBUTION

See Table 2 (p. 5).

GENUS LITHORNIS Owen, 1840

TYPE SPECIES

Lithornis vulturinus Owen, 1840, by monotypy.

INCLUDED SPECIES

Lithornis vulturinus Owen, *L. nasi* (Harrison, 1984), ?*L. hookeri* (Harrison, 1984), *L. promiscuus* n. sp., *L. plebius* n. sp., and *L. celetius* n. sp.

Lithornis Owen, 1840, p. 162 (erroneously cited by all subsequent authors as 1842; see *L. vulturinus:* "Comments"); Owen, 1841, p. 206, pl. XXI (erroneously cited as 1842 by Cracraft and Rich, 1972, and mistaken by all authors as the first valid description of the genus); Owen, 1845, p. 291; Owen, 1846, p. 549, figs. 232, 233; Knight, 1855, p. 474; Owen, 1861, p. 328; Wallace, 1876, p. 163; Nicholson, 1879, p. 266; Sharpe, 1884, p. 239; Prestwich, 1888, p. 354; Fürbringer, 1888, p. 1295; Lydekker, 1891 (in part), p. 34; Sharpe, 1891, p. 202; Geikie, 1893, p. 968; Beddard, 1898 (in part), p. 484; Lambrecht, 1928, p. 7; Lambrecht, 1933 (in part), p. 403, fig. 134; Brodkorb, 1964, p. 250; Cracraft and Rich, 1972, p. 280; Fisher and Peterson, 1971, pp. 52, 172; Swinton, 1975, p. 52; Harrison and Walker 1977, p. 28, fig. 12; Harrison, 1979, p. 7; Walker, 1980, p. 28; Olson, 1981, p. 167; Rich, 1983, p. 3; Houde, 1986, p. 563–565, figs. 1–3; Houde, 1987a, p. 126, 127; Houde, 1987b, p. 28.

Pediorallus Harrison and Walker, 1977, p. 36, fig. 13 (not pl. 7); Walker, 1980, p. 28; Harrison, 1984, p. 18, figs. 1–5. NEW SYNONYMY.

Promusophaga Harrison and Walker, 1977, p. 40, fig. 14, pl. 9; Walker 1980, p. 30. NEW SYNONYMY.

DIAGNOSIS

Distinguished from all other sufficiently known lithornithids by longer and more slender wing elements; also distinguished from *Paracathartes* by

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parallel, longitudinally arranged microscopic vascular canals in the compacta of the tibiotarsus; also distinguished from *Pseudocrypturus* by presence of large pterygoid fossa, absence of caudal process of palatine, and absence of vomer-premaxillae articulation.

LITHORNIS VULTURINUS Owen, 1840

Lithornis vulturinus Owen, 1840, p. 162 (erroneously cited by all authors as 1842; see "Comments"); Owen, 1846, p. 549, figs. 232, 233; Lydekker 1891 (in part), p. 34; Lambrecht 1933 (in part), p. 403, fig. 134.

Proherodius oweni Lydekker, 1891 (in part), p. 363, fig. 75 (not p. 60), incorrectly referred specimen.

Neptuniavis minor Harrison and Walker, 1977 (in part), p. 11 (not pl. 1), incorrectly designated paratype.

Parvigyps praecox Harrison and Walker, 1977 (in part), p. 31 (not pl. 7), incorrectly referred specimen.

Pediorallus barbarae Harrison and Walker, 1977, p. 36, fig. 13 (not pl. 7); Walker 1980, p. 29; Harrison, 1984, p. 18, figs. 1, 2. NEW SYNONYMY.

Promusophaga magnifica Harrison and Walker, 1977, p. 40, fig. 14, pl. 9. NEW SYNONYMY.

HOLOTYPE

Consisted of a partial sternum, thoracic vertebra, ribs, distal end of left femur, and proximal end of left tibiotarsus embedded in a clay nodule (Fig. 32); collected by J. Hunter before 1793; destroyed in World War II (Cracraft and Rich, 1972; Harrison and Walker, 1977); documented by two lithographs and one woodcut, figured by Owen (1841, 1846).

TYPE LOCALITY

Isle of Sheppey, Kent, England, TL. 955 738 – TM. 024 717.

HORIZON

Ypresian (Early Eocene), Division D-E of the London Clay, North Sea Basin.

NEOTYPE

BMNH A 5204 (Fig. 33): right humerus, radius, and ulna all lacking distal ends, right scapula, right half of sternum, distal ends of left radius and ulna, proximal end of left femur, proximal end of right tibiotarsus, vertebrae C.9,

C10, C12, C13, C15, and T1, ribs, and fragments all associated in a clay nodule; collected by J. S. Bowerbank, date unknown; from the type locality of *Lithornis vulturinus;* referred to *Promusophaga magnifica* (Musophagidae) by Harrison and Walker (1977). NEW DESIGNATION OF NEOTYPE.

REFERRED SPECIMENS

BMNH 33138: referred to *Lithornis vulturinus* by Lydekker (1891); holotype of *Promusophaga magnifica* Harrison and Walker, 1977; figured by Lambrecht (1933) and Harrison and Walker (1977). BMNH 38933: referred to *Lithornis vulturinus* by Owen (1846); referred to *Parvigyps praecox* by Harrison and Walker (1977); figured by Owen (1846). BMNH 33934: referred to *Promusophaga magnifica* by Harrison and Walker (1977). BMNH 38935: referred to *Promusophaga magnifica* by Harrison and Walker (1977). BMNH A 225: previously specimen #IGS GSM 4805; referred to *Proherodius oweni* by Lydekker (1891); paratype of *Pediorallus barbarae* Harrison and Walker, 1977; figured by Lydekker (1891) and Harrison and Walker (1977). BMNH A 3681: holotype of *Pediorallus barbarae* Harrison and Walker, 1977; figured by Harrison and Walker (1977). BMNH A 4270; paratype of *Neptuniavis minor* Harrison and Walker, 1977 (Procellariidae). BMNH A 5278: referred to *Pediorallus nasi* by Harrison (1984). BMNH A 5195: referred to *Pediorallus barbarae* by Harrison (1984). BMNH A 5197: referred to *Pediorallus barbarae* by Harrison (1984). BMNH A 5198: referred to *Pediorallus barbarae* by Harrison (1984). BMNH A 5199: referred to *Pediorallus barbarae* by Harrison (1984).

DIAGNOSIS

Larger than *Lithornis nasi, ?L. hookeri, L. celetius,* and *L. plebius,* smaller than *L. promiscuus;* pectoral crest of humerus more arcuate and lateral margins of sternum more divergent caudally than in all other sufficiently known species of this genus.

DISTRIBUTION

Known from Divisions C-E (Ypresian) of the London Clay in England.

COMMENTS

Lithornis Bowerbank, 1854 is a junior homonym of *Lithornis* Owen, 1840 and was renamed *Argillornis* by Owen in 1878 (Brodkorb, 1963). The genus *Argillornis* reportedly belongs with the pseudotoothed pelecaniform birds (Harrison and Walker, 1977) which are most recently included under the name Pelagornithidae (Olson, 1985).

Lithornis vulturinus was one of the first fossil birds known to science. It was collected before 1793 and described by Sir Richard Owen in 1840 in what is apparently the second publication ever to treat a fossil bird. The well known fossil horse, *Hyracotherium,* was described in the same paper. Students of avian paleontology have always cited this paper incorrectly as being

published in 1842 (the year the volume was bound), thus mistaking Owen's (1841) second paper on *Lithornis* as the original description of the species. In his original description, Owen (1840) attributed a fragmentary synsacrum, BMNH 38933, as well as the better known holotype, to *L. vulturinus*. Owen never included the synsacrum in subsequent discussions of *L. vulturinus* and in 1846 he commented that it possessed no characters of diagnostic value. In 1977 Harrison and Walker referred this synsacrum to the putative vulture, *Parvigyps praecox*, but, in fact, it does belong to *L. vulturinus*. It agrees in all details except size with the synsacra of *L. celetius* and *L. promiscuus*. It differs from the synsacra of vultures because it is not fused with the innominates and it lacks the pronounced ventral ridge of the preacetabular vertebrae that is characteristic of vultures. The synsacral vertebrae are also more uniformly spaced in vultures than they are in *Lithornis*.

Ironically, Owen (1841, 1846) remarked that *Lithornis* could not be related to "Struthious" birds because *Lithornis* possessed a carinate sternum. He considered the fossil closest to *Cathartes* (Vulturidae), although he made no distinction between New World and Old World vultures (Cracraft and Rich, 1972).

It is fortunate that the holotype was documented by illustrations before it became a victim of the Second World War. Two lithographs from somewhat different aspects were published by Owen in 1841 and an improved, more detailed woodcut of one of them appeared in Owen 1846 (Fig. 32, this paper). Harrison and Walker were of the opinion that the woodcut was cruder than the lithograph but from my comparisons with other lithornithid specimens I must disagree. The woodcut is, in fact, remarkably detailed and accurate. In contrast, Harrison and Walker's (1977) redrawn renditions of Owen's (1841) figures are inaccurate. Although Harrison and Walker represented them as natural size, their figures are actually fifty percent larger than Owen's. Note especially that what Harrison and Walker designate as the distal end of a tibiotarsus is actually the proximal end of the left tibiotarsus (correctly labeled in Owen's figure), almost in articulation with the femur. The lateral cnemial crest of the tibiotarsus was chipped, thus exposing the rounded lateral articular facet in Owen's (1841, 1846) figures. This was apparently the cause of the confusion as to the proper identification of the bone by Harrison and Walker (1977).

Lydekker felt that *Lithornis* was closer to the Accipitridae (i.e., *Accipiter* and *Circus*) than to the Vulturidae, but he considered its familial relationships uncertain. Lydekker (1891) correctly referred BMNH 33138 but incorrectly referred BMNH A 56, a fragmentary pelvis, to *L. vulturinus*. His interpretation of A 56 as the pelvis of a raptorial bird was justifiable because the postacetabular portion was short, as in modern Falconiformes. The postacetabular portion of the pelvis of *Lithornis* is, however, much longer.

An imperfect tarsometatarsus of *L. vulturinus*, BMNH A 225 (=IGS GSM 4805), was incorrectly referred to *Proherodius oweni* by Lydekker (1891) in the Addenda to his catalogue. This specimen was later designated as the paratype of *Pediorallus barbarae* (see below) by Harrison and Walker (1977).

This specimen has, unfortunately, been somewhat damaged by handling since it was originally illustrated and cast.

Lambrecht (1933) included *Lithornis* among the gypaetine accipitrids but he considered it as *incertae sedis*. He included BMNH 33138 and BMNH A 56 as well as another incorrectly identified specimen, BMNH A 71, the distal end of a humerus, in his figures of *L. vulturinus*. Apart from Harrison and Walker's (1977:32) account, there does not seem to be any published record that Owen ever referred A 71 to *L. vulturinus*. Harrison and Walker (1977) designated A 71 as the holotype of *Parvigyps praecox* (Accipitridae). In spite of its short medial epicondyle, I consider A 71 as possibly belonging with the Lithornithidae, but not *L. vulturinus*. It is certainly not an accipitrid because it lacks tricipital grooves. At any rate, it is too fragmentary to be of any taxonomic value of itself.

In 1977 Harrison and Walker reallocated all the specimens that had previously been assigned to *L. vulturinus*. They made BMNH 33138 the holotype of *Promusophaga magnifica*, supposedly the earliest known touraco (Musophagidae). The humerus of BMNH 33138 is, however, consistent with *Lithornis* and inconsistent with touracos because the pectoral crest forms a smooth arc and it is not flared distally, and the internal tuberosity is positioned dorsally on the shaft, not on the bicipital crest. Furthermore, the sternocoracoid process of the sternum is shorter than in touracos. To *P. magnifica* Harrison and Walker referred two topotypical specimens of *L. vulturinus*, BMNH 38934 and 38935. They made A 71 the holotype of *Parvigyps praecox*. The destroyed holotype of *L. vulturinus* itself was relegated to yet a third family and order, the Threskiornithidae (Plataleidae) of the Ciconiiformes (Ardeiformes).

Harrison and Walker (1977) mistakenly designated a femur of *L. vulturinus*, BMNH A 4270, as a paratype of *Neptuniavis minor* (Procellariidae). The femur of procellariids is characterized by an extremely broad and shallow rotular groove and diminutive medial condyle; both are well developed in A 4270, in perfect agreement with other specimens of *Lithornis*.

The proximal end of a tarsometatarsus of *L. vulturinus*, BMNH A 3681, was designated as the holotype of *Pediorallus barbarae* by Harrison and Walker (1977). However, there are no characters present on the fragmentary specimens of *Pediorallus barbarae* that can be used to unambiguously differentiate this species from either *L. vulturinus* or *L.* ("*Pediorallus*") *nasi*. I, therefore, consider *Pediorallus* to be a synonym of *Lithornis* in the absence of material that would indicate otherwise. I also consider *Pediorallus barbarae* to be synonymous with *Lithornis vulturinus* rather than with *L. nasi* because the holotype specimen of *P. barbarae* accords better with the range of size of *L. vulturinus* and because all positively identifiable (i.e., reasonably complete) specimens of *L. nasi* are geologically older. The hypotarsi of the holotype and paratype of *Pediorallus barbarae* do not possess osseous canals, like true rallids. The hypotarsi of these specimens are not eroded as reported by Harrison and Walker (1977) and Harrison (1984) and are, instead, characteristic of lithornithids. Two distal ends of humeri were referred to *Pedio-*

rallus by Harrison and Walker (1977). The distal end of a humerus, BMNH
A 4490, that was referred to *P. barbarae* (Harrison and Walker, 1977) belongs
to *Lithornis nasi*. Another distal end of a humerus, BMNH A 3679, that was
referred to *Pediorallus barbarae* (Harrison and Walker, 1977), belongs to
?*Lithornis hookeri* (Harrison, 1984). These distal humeri are consistent with
Lithornis but inconsistent with rails because they do not possess tricipital
grooves and both the capitulum (dorsal condyle) and medial epicondyle are
bulbous.

Cracraft and Rich (1972) wrote that because of the destruction of the
holotype, the correct systematic status of *L. vulturinus* would probably never
be known. They did, however, treat *Lithornis* as *"incertae sedis* near (or
within) the Accipitridae" and suggested that "it may be necessary to desig-
nate one of the referred specimens [BMNH 33138, A 56, or A 71] . . . as the
neotype" (p. 281).

The erection of a neotype for *L. vulturinus* is indeed warranted and is now
all the more justified for the following reasons: (1) Owen's illustrations
(1841, 1846) of *L. vulturinus* clearly show that this species is referrable to the
same group of paleognathous carinate birds lately recognized by Houde and
Olson (1981). Owen's name is the earliest applied to any member of the
group. (2) The identities of several similar species of lithornithids have been
and remain clouded with confusion due to erroneous descriptions of frag-
mentary specimens. Thus, this action is taken in connection with revisory
work. (3) The correct identity of *L. vulturinus* is confused by the presence of
two closely related species, referrable to this genus, collected at the type
locality. Owen's (1841, 1846) figures are equivocal and will never permit the
certain identification of one of these as the originally described species.
Thus, in order to describe these two species without consequently creating a
synonymy, it is necessary to arbitrarily designate one of them as *Lithornis
vulturinus*. The more common of the two species is chosen.

In order to erect a neotype, it must be demonstrated that the neotype is
indeed consistent with all that is known of the original holotype of *Lithornis
vulturinus*. This task is greatly facilitated by three facts: (1) Lithornithids
represent the most abundantly preserved family of fossil birds yet known
from the London Clay. (2) Although isolated and incomplete bones of *L.
vulturinus* have been misidentified, lithornithids are extremely distinctive
and difficult to confuse with other birds once the investigator has divorced
himself from the impetus to place them in families of modern birds. It is not
surprising that when improperly described as members of modern families,
fragmentary specimens of lithornithids have typically been regarded as
somehow unusual or uncharacteristic of those families. (3) The neotype
specimen and several others referrable to the same species were collected at
the type locality of *Lithornis vulturinus*.

The conditions for designating a neotype as set forth by Article 75 of the
International Code of Zoological Nomenclature (Adopted by the XV Inter-
national Congress of Zoology, London, July 1958) and Mayr (1969:372) are
satisfied because: (1) the holotype is known to have been destroyed (Cracraft

and Rich, 1972: Harrison and Walker, 1977); (2) the name *Lithornis vulturinus* is still in general use; (3) the systematic position and relationships of *L. vulturinus* are confused; and (4) the designation of the neotype is made in connection with revisory work.

Although the destroyed holotype and the neotype of *L. vulturinus* share practically no elements in common that can be compared, they can be shown, beyond doubt, to be consistent with one another in morphology. This is possible by comparisons with more complete skeletons of closely related species which do include elements in common with both the destroyed holotype and the neotype. Furthermore, the series of referred specimens from the type locality consist of some elements in common with both the destroyed holotype and the neotype. I chose BMNH A 5204 to be the neotype specimen in spite of the fact that it does not share elements in common with the destroyed holotype because it is the most completely preserved specimen available and it has not been previously designated as a type of some other taxon.

The published illustrations of the holotype are completely consistent with both North American and British specimens of *Lithornis*, which are in turn entirely consistent with the neotype. Although the most diagnostic characters of the family and genus are described above, a more detailed description of *Lithornis* is presented here specifically for all the elements that were included in the destroyed holotype. Birds of the genus *Lithornis* exhibit all of the following characters. Coracoid: with slender shaft; flat, dorsoventrally thin, and mediolaterally broad sternal extremity; long flared lateral process (angle); and a conspicuous intermuscular line close to the lateral margin of the ventral surface. Sternum: with few (four or five) costal processes; a small but distinct impression of the supracoracoideus muscle; a truncate posterior margin; and shallow coracoidal sulci. (In addition, *L. vulturinus* possesses a sternum with lateral margins that diverge posteriorly and a sternocoracoid process that is directed posterolaterally). Femora: with large rounded condyles in anterior view; a centrally placed rotular groove; and a shorter medial than lateral condyle. Tibiotarsus: with small and low anterior cnemial crest; relatively large and down-turned lateral cnemial crest. Although isolated bones belonging to other families of birds might be described by some of the characters listed here, no family possesses all of these characters in combination.

There are two species of *Lithornis* known from the type locality, but it is not clear to which of these Owen applied the name *Lithornis vulturinus*. The resolution of such a problem for the sake of nomenclatural stability and clarity is the most important criterion for the erection of a neotype. The ambiguity in the identification of the two species of *Lithornis* from the type locality of *L. vulturinus* results from their morphological similarity and Owen's failure to provide measurements of the holotype specimen. Owen's figures (1841, 1846) are said to be natural size and this is verified by comparison of BMNH 38933, a synsacrum also figured by Owen (1846). However, measurements of the sternum and lateral angle of the coracoid, taken from

Owen's figures (1841, 1846), accord with the size of the specimens referred here to *L. vulturinus*. Measurements of the femur and neck and medial angle of the coracoid accord with the topotypical BMNH A 5303, referred in this paper to *L. plebius*. I believe this resulted from the artist's attempt to add a perspective of depth to his figures. Thus, the true size of the original holotype specimen will never be known with certainty. In accordance with the guidelines for the designation of the neotype, I have made an arbitrary decision, based on the best available evidence, as to which of these two species should be treated as *Lithornis vulturinus*.

MEASUREMENTS
See Tables 4, 5, 9–13, 15, 16, 19–22, 24, and 25.

LITHORNIS NASI (Harrison, 1984), NEW COMBINATION

Pediorallus nasi Harrison, 1984, p. 19–21, figs. 3–5.

HOLOTYPE
BMNH A 5200 (Figs. 24G and 25D): associated extreme proximal fragments of left humerus, and right ulna, extreme distal fragments of right femur and right tibiotarsus, and two thoracic vertebrae; collected by W. George in 1977.

TYPE LOCALITY
Walton on the Naze, Essex, England, TM. 267 243.

HORIZON
Ypresian (early Eocene), Division A, London Clay, North Sea Basin.

REFERRED SPECIMENS
BMNH A 5201: referred to *Pediorallus nasi* by Harrison (1984). BMNH A 5279: referred to *Pediorallus nasi* by Harrison (1984). WN 74067–8: figured by Daniels (1979, p. 7). WN 75071: figured by Daniels (1979, p. 12, pl. I, VI). WN 75124: figured by Daniels (1979, p. 21, pl. VII). WN 75127: figured by Daniels (1979, p. 22). WN 79238: figured by Daniels (1979, p. 49, pl. IX, X). WN 81373. WN 82403. WN 83420. WN 83445. PU 23482: provisionally referred here. BMNH A 5455: provisionally referred here. UM 73103 (Figs. 23B and 26F): provisionally referred here. MMH.V.P. 1285 A: tentatively referred to the Galliformes by Hoch (1973); figured by Hoch (1973, pl. 7); provisionally referred here.

DIAGNOSIS
Smaller than *Lithornis vulturinus*, *L. celetius*, and *L. promiscuus*; larger than ?*L. hookeri* and *L. plebius*.

DISTRIBUTION

Positively identifiable specimens (i.e., sufficiently complete) of this species are known only from Division A of the London Clay. However, it probably occurs throughout Ypresian beds of the North Sea depositional basin, including Divisions A–E of the London Clay in England and the Plastic Clay of Denmark. Specimens from the Wasatchian in the Willwood Formation of Wyoming may also belong to this species.

COMMENTS

Essentially the entire appendicular skeleton of this species is known from a composite series of bones, most of which were collected from the type locality and figured by Daniels (1979). Many specimens differ slightly in size, the exact configurations of the coracoid and the iliotrochanteric insertions on the femur, the robustness of the tarsometatarsus, and probably in other respects as well. These variants, however, are all well within the range of intraspecific variation of neospecies of tinamous.

This species is presumed to have been sympatric with *Pseudocrypturus cercanaxius* at the Walton locality.

Lithornis nasi was originally described in the genus *Pediorallus* by Harrison (1984). The type species of *Pediorallus* (*P. barbarae*), however, cannot be distinguished from *Lithornis vulturinus* (or for that matter from *L.* [*"Pediorallus"*] *nasi;* see comments under *Lithornis vulturinus*) with which I consider it to be synonymous. I, therefore, do not recognize the validity of the genus *Pediorallus*.

The distal end of a femur, BMNH A 5278, was referred to *Pediorallus nasi* by Harrison (1984) but it is too large to belong to *P. nasi*. It belongs instead to *Lithornis vulturinus*.

A humerus of *L. nasi* from the Plastic Clay in Denmark, MMH.V.P. 1285 A, was figured by Hoch (1973, pl. 7). Hoch commented on similarities of this humerus, for example its lack of tricipital grooves, to those of ostriches and tinamous. She, nevertheless, tentatively assigned the specimen to the phasianoid Galliformes.

A specimen including a cranium, femur, tarsometatarsi, vertebrae, and other fragments, UM 73103, from the Wasatchian (Early Eocene) of Wyoming, cannot be distinguished from *Lithornis nasi* on the basis of these elements. It is tentatively referred here to this species, together with a proximal end of a tarsometarsus, also from the Wasatchian of Wyoming.

MEASUREMENTS

See Tables 3, 4, 7–11, 13–16, and 19–25.

?LITHORNIS HOOKERI (Harrison, 1984), NEW COMBINATION

Pediorallus hookeri Harrison, 1984, p. 21.
Pediorallus barbarae Harrison and Walker (in part), 1977, p. 36 (not pl. 7),
    incorrectly referred specimen.

SYSTEMATIC PALEONTOLOGY

HOLOTYPE

BMNH A 5202 (Fig. 25E): distal end of a tibiotarsus; collected by J. Hooker in 1980.

TYPE LOCALITY

Warden Point, Isle of Sheppey, Kent, England, TL. 955 738 – TM. 024 717.

HORIZON

Ypresian (Early Eocene), Division D–E, London Clay, North Sea Basin.

REFERRED SPECIMENS

BMNH A 3679: referred to *Pediorallus barbarae* by Harrison and Walker (1977). BMNH A 3701: referred to *Pediorallus hookeri* by Harrison (1984). BMNH A 4278: referred to *Pediorallus hookeri* by Harrison (1984). BMNH A 5421.

DIAGNOSIS

Smaller than all other currently known species of Lithornithidae.

DISTRIBUTION

Known from Divisions B–E (Ypresian) of the London Clay in England.

COMMENTS

This species is known only from a composite series of a distal end of a humerus, proximal end of a femur, distal end of a tibiotarsus, and proximal ends of tarsometatarsi.

?*Lithornis hookeri* was originally described in the genus *Pediorallus* by Harrison (1984). The type species of *Pediorallus*, however, cannot be distinguished from *Lithornis vulturinus*, with which I consider it to be synonymous. Similarly, "*Pediorallus*" *hookeri* is represented by insufficient remains to be distinguished from either *Lithornis* or *Pseudocrypturus* at the generic level. Its allocation at this time to *Lithornis*, rather than *Pseudocrypturus*, is somewhat arbitrary but preferred because of the closer similarity of the origin of the antebrachial flexors on the medial epicondyle to *Lithornis* than to *Pseudocrypturus*. The condition of the origin of the flexor muscles on the epicondyle is not cited as a character that can be used to diagnose *Pseudocrypturus* from *Lithornis* because this region is well preserved in only one positively identifiable specimen of *Pseudocrypturus* and thus may not be characteristic of the genus.

A distal humerus, BMNH A 3679, was incorrectly referred to a much larger lithornithid, *Pediorallus barbarae* (=*Lithornis vulturinus*), by Harrison and Walker (1977). This is the only specimen referred to ?*L. hookeri* here that was not collected at the type locality of the species. It comes, instead, from the "Fish Tooth Beds" of Bognor Regis, Sussex, England, SZ.920 979 – SZ. 924 983, and may be somewhat older (Division ?B, London Clay) than the other specimens of this species.

SYSTEMATIC PALEONTOLOGY

MEASUREMENTS
See Tables 11, 19–21, and 24.

LITHORNIS CELETIUS, new species

HOLOTYPE
USNM 290601 (Figs. 2, 4, 21B, C, 23A, and 24A): loosely associated skull, quadrates, pelvis in several pieces, right femur lacking distal end, radiales, and caudal vertebra; collected by A. Houde and P. Houde in August 1979.

TYPE LOCALITY
Bangtail Quarry, NW 1/4 of NE 1/4 Sec. 6, T1S R8E, Sedan Quadrangle, Park County, Montana.

HORIZON
Earliest Tiffanian (late Paleocene), Fort Union Formation, western Crazy Mountain Basin.

ETYMOLOGY
From the Greek *keletion*, a race horse, for which the type locality, Bangtail, is also named.

REFERRED SPECIMENS
USNM 290554 (Figs. 12A, 13A, 14B, 20A, 26C, and 28–30; see Houde, 1986, fig. 3; Houde, 1987a, p. 126). USNM 336200 (Figs. 8 and 18A). PU 16961 (Figs. 9, 23C, 24B, 26A, and 27A). PU 23483 (Fig. 15A). PU 23484 (Figs. 14A and 26B). PU 23485 (Figs. 15B, 17A, and 21A). PU 20510. UM 83891.

DIAGNOSIS
Larger than *Lithornis nasi*, ?*L. hookeri*, and *L. plebius;* smaller than *L. vulturinus* and *L. promiscuus;* differs from *L. vulturinus* in its humerus with less arcuate pectoral crest and sternum with short sternocoracoid process and more parallel lateral margins. Further distinguished from *L. promiscuus* by narrower supraorbital region. Distinguished from all other lithornithids by tarsometatarsus with inner metatarsal narrow and raised and with narrow cotylae and by ilium and ischium which *may* meet but not necessarily fuse to form an enclosed ilioischiadic foramen.

DISTRIBUTION
Known from the Tiffanian of both the Fort Union Formation in Montana and the Polecat Bench Formation in Wyoming.

COMMENTS
Remains of *Lithornis celetius* and large amounts of its eggshell were first discovered at the Bangtail site in 1952 by William J. McMannis during his survey of the Bridger Range and adjacent areas.

Essentially the entire skeleton of this species is known from a composite series of bones, representing a minimum of two individuals, that were collected at Bangtail Quarry. Although these remains were only questionably associated, individual bones being preserved in small isolated nodules, the two individuals can be fairly confidently separated by size. Morphological differences between the two individuals include dorsoventral height of the ilium, flattening of the ulna, and elevation of the tarsometatarsal trochleae but these differences are within the range of individual variation of individual species of tinamous. The two individuals are grouped as seven specimens (the holotype and all the referred material except PU 20510 and UM 83891) because parts were collected at different times for different institutions and not all parts could be confidently assigned to either one individual or the other.

A ground lapidary thin section of a tibiotarsus (USNM 290554) was made (Houde, 1987a) and figured (Houde, 1986, fig. 3; also Figs. 28–30, this paper).

The eggshells of *L. celetius* (included in PU 16961) are glossy with large, widely spaced pores, clearly visible to the naked eye. The eggshells closely resemble those of *Rhynchotus rufescens,* but are much thicker. Radial thin sections of the eggshell (Fig. 31) reveal the following. There is an outer layer that resembles the cuticular layer of true shell described by Tyler and Simkiss (1959) for *Rhea.* Tyler and Simkiss used stains to study eggshells, whereas the eggshells I examined were not stained. Tinamous also exhibit a superficial layer in unstained eggshells like that of *Lithornis,* but Tyler and Simkiss made no mention of a cuticular layer of true shell in tinamous. Whether or not this superficial layer is homologous to the one described in *Rhea,* it is part of the true shell and could not be cuticle *per se* in the fossils. The fossil eggs also have simple conical pores like those of tinamous, and another unnamed band or layer of different color in the unstained shell, just superficial to the mamillary bodies, again as in the unstained eggshell of tinamous.

Lithornis celetius probably exhibited the same mating system of simultaneous polygyny and sequential polyandry as seen in tinamous and most ratites. See comments under *L. promiscuus,* of which more eggshell caches are known.

MEASUREMENTS
See Tables 3–5, 8–11, 13–20, and 22–26.

LITHORNIS PROMISCUUS, new species

HOLOTYPE
USNM 336535 (Figs. 2, 4, 6, 7C, D, 8, 10, 11, 12B, 13B, 14C, 16A, 17B, 18B, 19A, 20B, 21E, F, 22, 23D, 24C, D, 25A, 26D, 27B, and 41): associated quadrates, fragmented mandible and premaxillae, coracoids, scapulae, sternum, furcula, left and distal end of right humeri, left and broken right ulna, ulnares, left radiale, right and broken left carpometacarpi, vertebrae C1, C2, C4–C6, C8, C15, T1, T3, T5–T7, synsacrum-Cc2, and pygostyle, right and

partial left innominates, broken left and proximal end of right femora, right and proximal end of left tibiotarsus, right and partial left tarsometatarsus, and an assortment of ribs, alar and pedal phalanges, and fragments; collected by A. Houde and P. Houde in July 1983.

TYPE LOCALITY
NE 1/4 of SE 1/4 Sec. 7, T56N R101W, Clark Quadrangle, Park County, Wyoming.

HORIZON
Plesiadapis cookei zone, middle Clarkforkian (earliest Eocene), Sand Coulee Beds, Willwood Formation, Clark's Fork Basin.

ETYMOLOGY
The name alludes to the presumed polygamous mating behavior of these birds.

REFERRED SPECIMENS
USNM 336570: an egg. USNM 391983 (Figs. 2, 4). UM 69343. AMNH 21900. AMNH 21901.

DIAGNOSIS
Larger than all other currently known species of *Lithornis;* further distinguished from *L. celetius* by its broader supraorbital region and the ilium and ischium which clearly do not meet caudally; further distinguished from *L. plebius* by its pygostyle with a clublike ventral process.

DISTRIBUTION
Known only from the Clarkforkian of the Willwood Formation in and near the type locality, T56N R101W, Park County, Wyoming.

COMMENTS
An unidentified distal end of a tarsometatarsus (UM 69343) of this species was briefly mentioned by Rose (1981) as the only known bird from Clarkforkian sediments. More recent collecting by Anne Houde and myself resulted in the discovery of the balance of the skeleton of that specimen as well as numerous other Clarkforkian birds. Essentially the entire skeleton of *L. promiscuus* is now known from several specimens. Individuals vary slightly in overall size and the ischium of one specimen (AMNH 21900) is narrower than that of the holotype (USNM 336535). It is possible that the supraorbital width of the frontal bones varies between different individuals as it does in some tinamous.

Fossils of *Lithornis promiscuus* are usually found in association with large caches of eggshell. All but a select few eggshells were, unfortunately, destroyed during acid preparation of the fossil bones. One egg of *L. promiscuus* (USNM 336570) is approximately 65 mm by 45 mm but it is

embedded in rock and difficult to measure accurately. I attribute the caches of eggshell to individual clutches of eggs, although the caches probably do not represent nests *per se*. I interpret the large clutches as indicative of the same polygamous mating system that is prevalent among extant paleognathous birds, in which several females contribute eggs to the nest of a single male. The eggs and my interpretation of the birds' behavior is discussed in more detail on page 118.

Lithornis promiscuus was sympatric with *L. plebius* in the Clarkforkian of North America. The holotypes of both species were associated with one another. *L. promiscuus* is usually found in association with *L. plebius*, and *L. plebius* has never been found without *L. promiscuus* except for the possible European specimen, BMNH A 5303. Although it is possible that *L. promiscuus* and *L. plebius* represent the different sexes of a single dimorphic species it is more conservative to treat them as a separate species. Significant differences in their morphology are cited in the diagnoses. Linear measurements of *L. plebius* are only 75% of those of *L. promiscuus*. The vast difference in their size greatly exceeds that exhibited by dimorphic modern paleognathous birds. Moreover, there are no other species pairs of lithornithids with a similar size difference.

The holotype of *Lithornis promiscuus* was also found in association with *Eobucco* sp., an as yet undescribed small bee-eater-like coraciiform bird, several small insectivorous mammals including *Ceutholestes dolosus*, and several small lizards.

MEASUREMENTS

See Tables 3–26.

LITHORNIS PLEBIUS, new species

HOLOTYPE

USNM 336534 (Figs. 4, 12C, 13C, 14D, 15C, 17C, 19B, 20C, 21D, 23E, 24E, 25B, 26E, and 27C): associated cranium in two pieces, dentary, quadrates, partial furcula, left and partial right coracoids, scapulae, right humerus, ulnae, fragmented radii, ulnare, carpometacarpi, vertebrae C2, C8–C10, C14, C15, T4–T6, T8, partial synsacrum, and pygostyle, partial innominates, femora, tibiotarsi, fibulae, left tarsometatarsus, and few phalanges; collected by A. Houde and P. Houde in July 1983.

TYPE LOCALITY

NE 1–4 of SE 1–4 Sec. 7, T56N R101W, Clark Quadrangle, Park County, Wyoming.

HORIZON

Plesiadapis cookei zone, middle Clarkforkian (earliest Eocene), Willwood Formation, Clark's Fork Basin.

SYSTEMATIC PALEONTOLOGY

ETYMOLOGY
From the Latin *plebs,* the common people, inferring a lesser status of this species than the larger and more impressive, sympatric *L. promiscuus.*

REFERRED SPECIMENS
UM 83892. BMNH A 5303. AMNH 21902. AMNH 21903.

DIAGNOSIS
Significantly smaller than all other currently known species of *Lithornis* except ?*L. hookeri;* larger than ?*L. hookeri;* further distinguished from *L. promiscuus* by its pygostyle with a pointed ventral process and from *L. promiscuus* and *L. celetius* by its more tapered caudal ischium.

DISTRIBUTION
Known from the Clarkforkian of the Willwood Formation in Wyoming and probably from Divisions D–E (Ypresian) of the London Clay in England.

COMMENTS
This species is known from all major appendicular elements.

Lithornis plebius was sympatric with *L. promiscuus* in the Clarkforkian of North America. The holotypes of both species were associated with one another. *L. promiscuus* is usually found in association with *L. plebius,* and *L. plebius* has never been found without *L. promiscuus* except for the possible European specimen, BMNH A 5303. Although it is possible that *L. promiscuus* and *L. plebius* represent the different sexes of a single dimorphic species it is more conservative to treat them as separate species. Significant differences in their morphology are cited in the diagnoses. Linear measurements of *L. plebius* are only 75% of those of *L. promiscuus.* The vast difference in their size greatly exceeds that exhibited by dimorphic modern paleognathous birds. Moreover, there are no other species pairs of lithornithids with a similar size difference.

Although eggshell has been found associated with all the known specimens of *L. plebius* from North America, these specimens were all found in association with *L. promiscuus. L. promiscuus,* however, has been found associated with eggshell in the absence of *L. plebius.* Since only one size of egg has yet been identified in these associations, it must be attributed to *L. promiscuus* and not *L. plebius.*

One putative specimen of *L. plebius* from the Isle of Sheppey in England, BMNH A 5303, includes elements of the pectoral girdle and appendage but none of the hindlimb. Its coracoid, humerus, and radius are morphologically identical to those of topotypical specimens of *L. plebius.* The humerus of the British specimen is very slightly smaller than those of the topotypical specimens of *L. plebius,* however. This specimen is referred to *L. plebius* in the interest of taxonomic and nomenclatural conservatism.

See comments on *L. promiscuus* for list of other vertebrates found in association with the holotype of *L. plebius.*

SYSTEMATIC PALEONTOLOGY

MEASUREMENTS
See Tables 3, 4, and 7–25.

PSEUDOCRYPTURUS, new genus

TYPE SPECIES
Pseudocrypturus cercanaxius n. sp., the only known species of this genus.

ETYMOLOGY
From the Latin *pseudo*, false, and *crypturus*, a tinamou.

DIAGNOSIS
Distinguished from all other currently known species of Lithornithidae by its: short appendages; robust lateral nasal bar; small pterygoid fossa; palatine with caudal process; vomer that articulates with the premaxillae; sternum with shallow notches in the posterior margin; coracoid with long slender shaft; scapula with straighter shaft and more pronounced acromion; tarsometatarsus with symmetrical middle trochlea and wing-like processes on medial and lateral cotylae; and pygostyle with short ventral process. Also distinguished from *Paracathartes* by its narrow scapula.

PSEUDOCRYPTURUS CERCANAXIUS, new species

HOLOTYPE
USNM 336103 (Fig. 3): associated skull, mandible, and nine cervical vertebrae; collected in 1975; figured by Houde and Olson (1981) and Siber (1982).

TYPE LOCALITY
Tynsky Quarry, Sections 16 and 22, T22N R117W, Kemmerer Quadrangle, Kemmerer, Lincoln County, Wyoming.

HORIZON
Late Wasatchian (Early Eocene), Fossil Butte Member, Green River Formation.

ETYMOLOGY
From the Greek *kerkion*, tail, and *anaxios*, worthless, referring to the rudimentary pygostyle exhibited by this species.

REFERRED SPECIMENS
USNM 336574; cast of specimen privately owned by Siber and Siber (Figs. 34 and 35; see "comments"). BMNH A 4490; provisionally referred here; referred to *Pediorallus barbarae* by Harrison and Walker (1977); referred to *Pediorallus nasi* by Harrison (1984). BMNH A 5424. WN 80280 (Figs. 12D, 13D, 14F, 15D, E, F, 18D, 20D, 21G, 23F, 24F, 25C, 26H, I, J, 27D, and E).

USNM 336576: a cast of WN 80280. WN 84474: provisionally referred here (see "comments").

DIAGNOSIS
As for the genus.

DISTRIBUTION
Known from the Wasatchian of the Green River Formation in Wyoming and Divisions A–E (Ypresian) of the London Clay in England.

COMMENTS
The entire skeleton, except the pelvis and caudal vertebrae, of this species is known from an articulated specimen belonging to Siber and Siber, Zurich, Switzerland. Two additional nearly complete skeletons, WN 80280 and WN 84474, were collected by M. C. S. Daniels from Division A of the London Clay at Walton on the Naze, Essex, England. Daniels' specimens, upon which the diagnosis of *Pseudocrypturus* is based in part, are only provisionally referred here because they are difficult to compare with the badly crushed material from the type locality of *Pseudocrypturus cercanaxius*. They are referred to this taxon primarily because of their short wings, long coracoids, and symmetrical middle trochlae of the tarsometatarsus. It is unclear from the Green River specimens whether the "winged" condition of the tarsometatarsal cotylae is a valid generic character.

Based on Daniels' material, this species is presumed to have been sympatric with *Lithornis nasi* at the Walton locality.

The crushed skull of *Pseudocrypturus cercanaxius* (USNM 336103) and its reconstruction were figured by Houde and Olson (1981). In those figures the vomer was incorrectly shown not to articulate with the premaxillae, as that part of the reconstruction was based on the condition in *Lithornis celetius* which differs *Pseudocrypturus cercanaxius*. New preparation of *Pseudocrypturus cercanaxius* reveals that the vomer and premaxillae probably do articulate, as shown in Fig. 6 of this paper.

MEASUREMENTS
See Tables 3–14, 16, 19–22, and 24–26.

GENUS PARACATHARTES Harrison, 1979

Paracathartes Harrison, 1979, p. 9, fig. 1; Rich, 1983, p. 3; Houde, 1986, pp. 563–565, figs. 1–3; Houde, 1987a, pp. 126–127.

TYPE SPECIES
Paracathartes howardae Harrison, 1979, the only known species of this genus.

SYSTEMATIC PALEONTOLOGY

DIAGNOSIS

Distinguished from all other sufficiently known genera of this family by stout scapula, humerus, radius, and ulna, coracoid with indistinct attachment for acrocoracohumeral ligament and scapular cotyla that faces more dorsally, pygostyle that lacks a ventral process, and circular arrangement of microscopic vascular canals in compacta of tibiotarsus; also distinguished from *Pseudocrypturus* by large pterygoid fossa and palatine that lacks caudal process.

PARACATHARTES HOWARDAE Harrison, 1979

Paracathartes howardae Harrison, 1979, p. 9, fig. 1; Rich, 1983, p. 3; Houde, 1986, pp. 563–565, figs. 1–3; Houde, 1987a, pp. 126–127.

HOLOTYPE

ROM 22658: distal end of a left tibiotarsus; collected by G.E. Lindblad and G. Sternberg on 4 August 1949; figured by Harrison (1979).

TYPE LOCALITY

In or near SW 1/4 Sec. 12, T50N R94W, northernmost branch of Elk Creek, SW of Basin, Wyoming.

HORIZON

Greybullian, middle Wasatchian (Early Eocene), Willwood Formation, Bighorn Basin.

REFERRED SPECIMENS

UM 76547. USNM 336564: three eggs. USNM 361402–361446 (USNM 361406: Figs. 26K and 27H; 361407: figured by Houde 1986, 1987a; 361408: Fig. 25F; 361412: Figs. 23G and 24H; 361415: Fig. 5; 361417: Figs. 12E and 13E; 361419: Fig. 14E; 361420: Figs. 16C and 17D; 361421: Figs. 16B and 17E; 361425: Fig. 19D; 361426: Fig. 19C; 361437: Fig. 7B; 361441: Fig. 18E; and 361445: Fig. 20E). USNM 391984 (Fig. 5). USNM 404747–404806 (USNM 404758: Fig. 7A).

DIAGNOSIS

As for the genus.

DISTRIBUTION

Known only from the Wasatchian of the Willwood Formation in the Bighorn Basin of Wyoming.

COMMENTS

This species was thought by Harrison (1979) to represent the earliest known cathartid vulture. Rich (1983) correctly doubted this allocation. The holotype is distinguishable from cathartid vultures because the tendinal

groove is positioned on the medial side of the anterior face of the shaft and the osseous tendinal bridge is absent, among other characters.

The entire skeleton of this species, except the sternum and pelvis, is known from a composite series of bones (USNM 361402–361446, 391984, 404747–404806) representing a minimum of five individuals which were preserved in a single large calcareous nodule.

An avian neurocranium (USNM 361415) was associated with the bones of *Paracathartes* in the large calcareous nodule but its identity remains uncertain because the bones of a new ?phorusrhacid were also present. The cranium is consistent with the other lithornithid material in its unfused coronal suture, large occipital condyle, and the relationship of the cotylae for the quadrate and pneumatic foramina in the tympanic cavity. Broad basipterygoid processes (not visible in Fig. 5) appear to have been present, as in other lithornithids. The opening for the eustachian tubes, which are characteristically widely separated in paleognathous birds, are not visible because the skull is badly crushed. This neurocranium is unlike the skulls of other lithornithids, however, with respect to its large rounded postorbital process, large and deep pseudotemporal fossa, and large tympanic cavity. These characters, which set this specimen apart from other lithornithids, are distinctly similar to the condition seen in many ratites. The question of whether the large postorbital process, pseudotemporal fossa, and tympanic cavity of this cranium represent a derived character state that further unites *Paracathartes* with ratites or instead represents a convergently ratite-like state of the Phorusrhacidae can only be conclusively resolved with the discovery of additional fossil material.

Three whole eggs (USNM 336564) and additional eggshell were found nearby within another calcareous nodule and are probably those of *P. howardae*. No other avian fossils are known from this immediate vicinity. Although much larger, the eggs resemble those of *Lithornis* both macroscopically and microscopically. One of the eggs is approximately 60 mm by 85 mm but it is embedded in rock and difficult to measure accurately.

A ground lapidary thin section of a tibiotarsus (USNM 361407) was made (Houde, 1987a) and figured (Houde, 1986, fig. 3; Figs. 28–30, this paper).

MEASUREMENTS
See Tables 3, 4, 7–13, 15–17, and 19–26.

SPECIES OF *INCERTAE SEDIS*

REFERRED SPECIMENS
YPM 883. AMNH 2633. BMNH A 4959. BMNH A 5203. BMNH A 5422. BMNH A 5423. BMNH 14633. BMNH 43165. WN 78210B.

COMMENTS
A poorly preserved distal end of a tibiotarsus, YPM 883, collected by Hunting and Chew in 1873, represents the youngest lithornithid fossil yet

known, assuming the specimen data are correct. It is from Bridgerian (middle Eocene) sediments of Henry's Fork in the Bridger Basin, Wyoming.

A specimen of an immature lithornithid (WN 78210 B: Figs. 12F, 13F, 14G, 15G, 18C, 26G, 27F, and 27G) from Walton on the Naze, Essex, England probably represents a second species of *Lithornis* from that locality. It is not described as new species because, as a single immature specimen, it may not be morphologically typical of its species. It differs notably from other lithornithids because its coracoid is thicker and more curved along the sternal end.
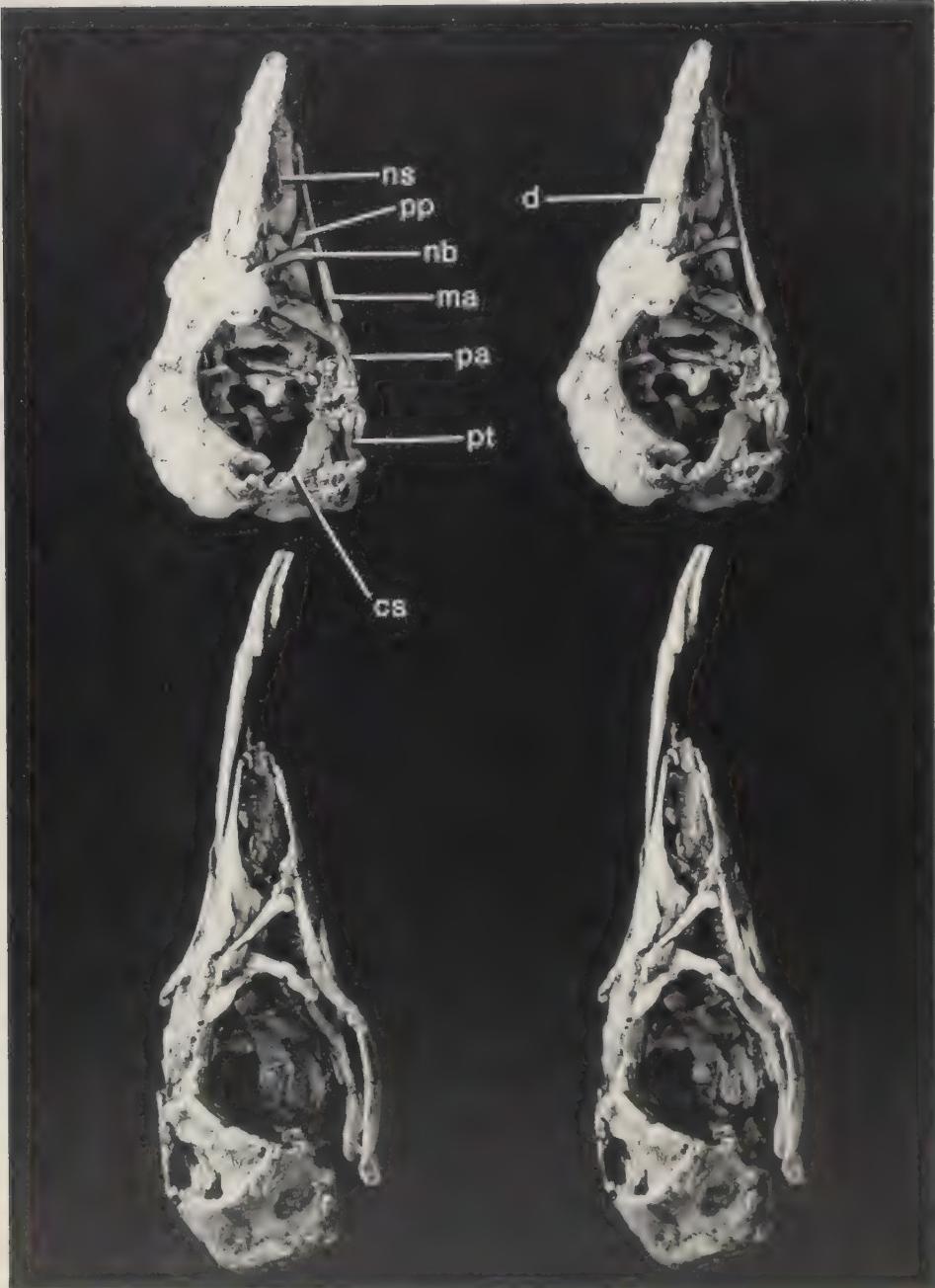
Fig. 2. Right lateral aspect of lithornithid skulls. Upper stereo image: *Lithornis celetius*, lacking rostral bill (holotype USNM 290601); lower stereo image: *Lithornis promiscuus* (USNM 391983); both coated with ammonium chloride. Abbreviations: cs—coronal suture (disarticulated), d—depression in dorsal nasal bar, ma—maxilla, nb—lateral nasal bar, ns—nasal septem, pa—palatine, pp—palatine process of maxilla, pt—pterygoid.

Fig. 3.   Right lateral aspect of the skull of *Pseudocrypturus cercanaxius* (holotype USNM 336103), natural size. Lower image: cut-out of skull to show the caudal process of the palatine (cp).
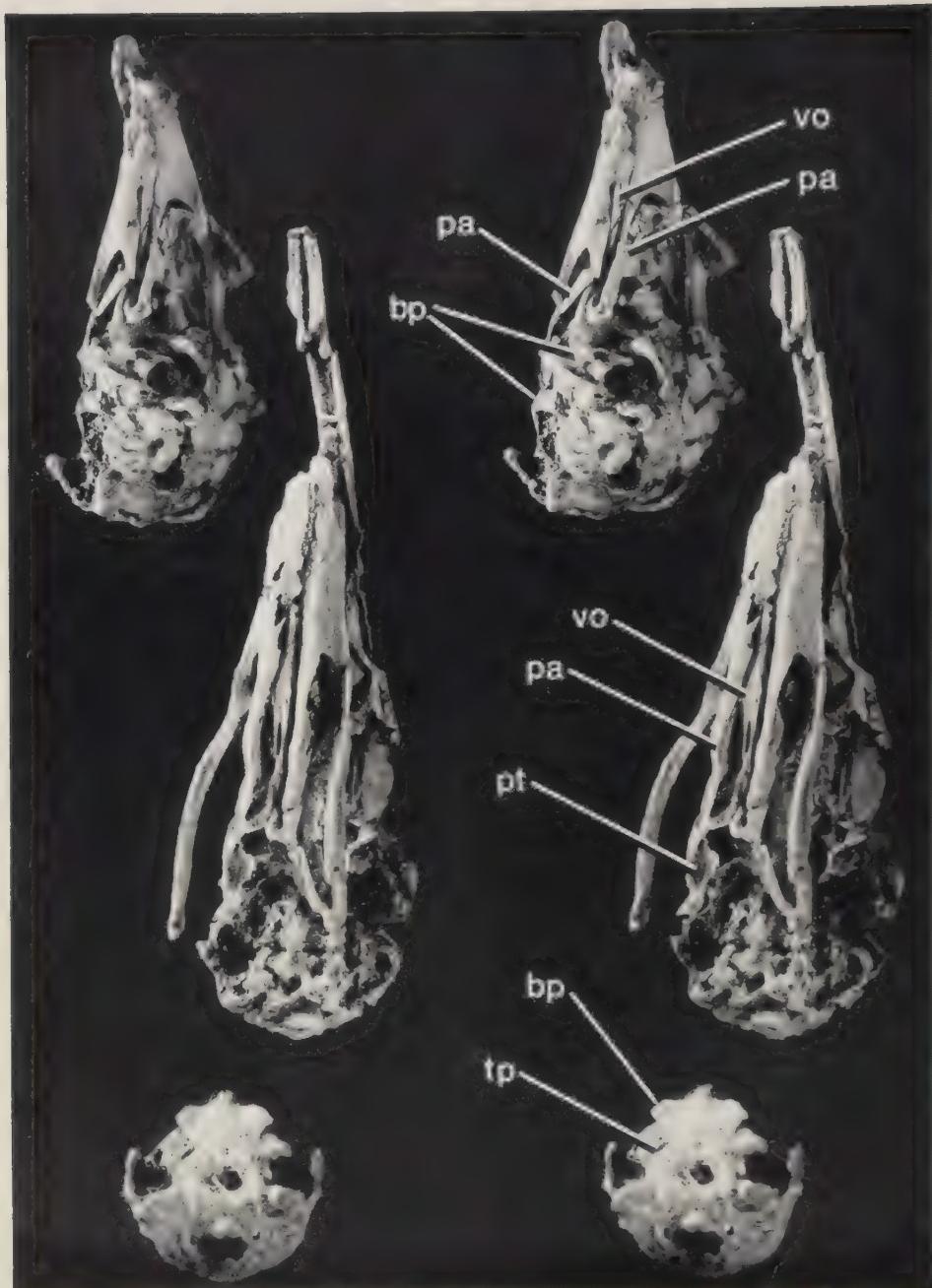
Fig. 4. Ventral aspect of lithornithid skulls. Upper stereo image: *Lithornis celetius* (holotype USNM 290601); middle stereo image: *Lithornis promiscuus* (USNM 391983; lower stereo image: neurocranium of *Lithornis plebius* (holotype (USNM 336534); all natural size and coated with ammonium chloride. Abbreviations: bp—basipterygoid process, pa—palatine, pt—pterygoid, tp—tuba pharyngotympanicus (eustachian tube), vo—vomer.

Fig. 5. Skull of *Paracathartes howardae*. Upper stereo image: ventral aspect of neurocranium presumed to belong to *Paracathartes howardae* (USNM 361415), natural size; middle stereo image: ventral aspect of palatal complex (USNM 391984), twice natural size; lower stereo image: dorsal aspect of palatal complex (USNM 391984), twice natural size; all coated with ammonium chloride. Abbreviations: ab—facet on pterygoid for articulation of basipterygoid, aq—facet on pterygoid for articulation of quadrate, pf—pterygoid fossa.
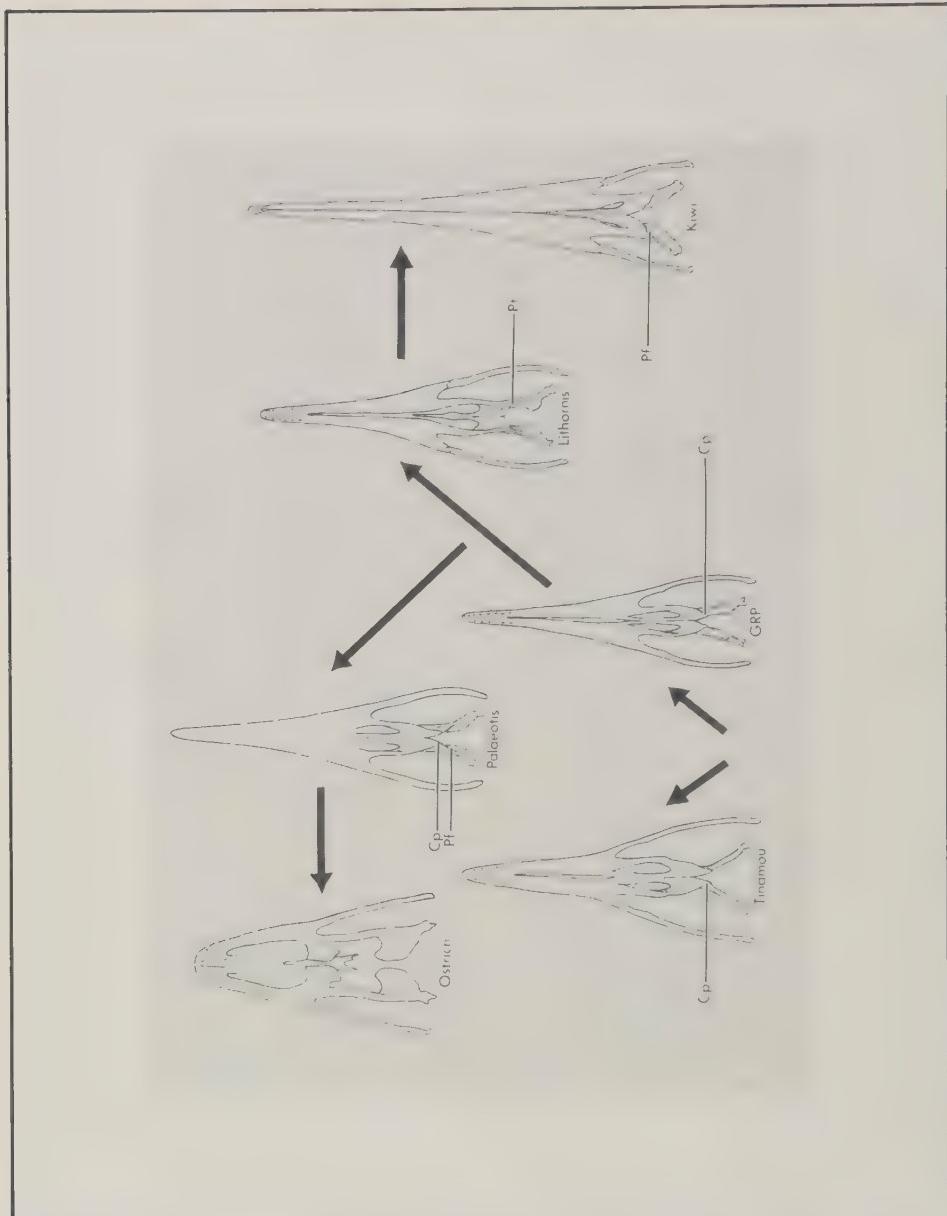
Fig. 6.   Ventral aspect of palates of lithornithids and selected other paleogna-
thous birds (reproduced from Houde, 1986). Arrows indicate hypothetical path of the
evolution in grades of the palatal complex in a tinamou (*Tinamus*, drawn from
USNM 345738), *Pseudocrypturus cercanaxius* ("GRP") (drawn from holotype
USNM 336103), *Lithornis promiscuus* (drawn from USNM 391983; agrees with
Paracathartes howardae, USNM 391984), *Palaeotis weigelti* (drawn from HLMD Me
7530), a kiwi (*Apteryx australis*, drawn from USNM 19025), and an ostrich (*Struthio
camelus*, drawn from USNM 224852), not to scale. Abbreviations: cp—caudal proc-
ess of palatine, pf—pterygoid fossa.
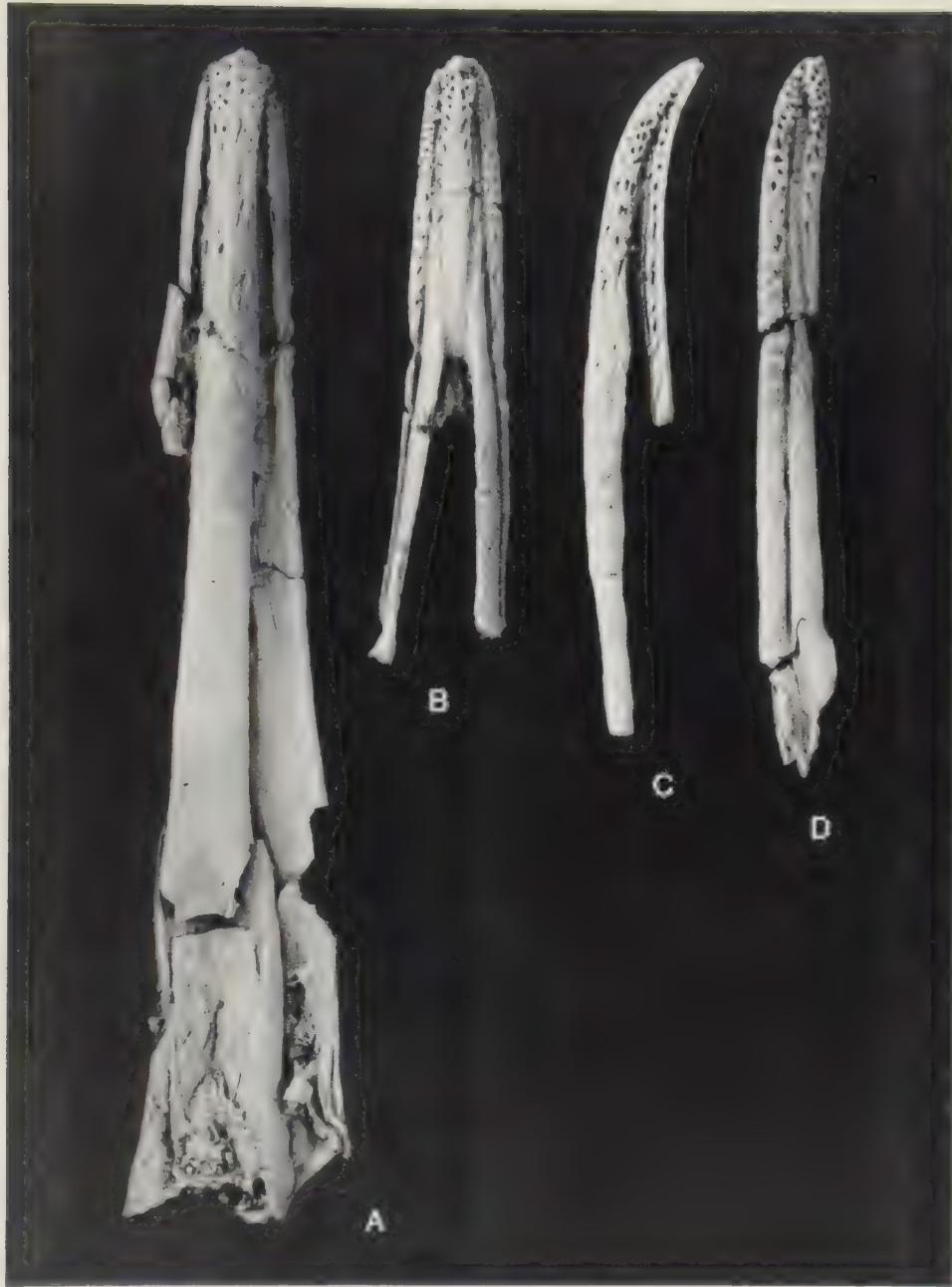
Fig. 7.   Lithornithid bills. A. Dorsal aspect of upper bill of *Paracathartes howardae* (USNM 404758). B. Ventral aspect of rostral mandible of *Paracathartes howardae* (USNM 361437). C. Right lateral aspect of premaxilla of *Lithornis promiscuus* (holotype USNM 336535). D. Right lateral aspect of rostral mandible of *Lithornis promiscuus* (holotype USNM 336535). All twice natural size and coated with ammonium chloride. Note the foramina for rostral rami of the mandibular nerve and the "W" pattern formed by rhamphothecal grooves.
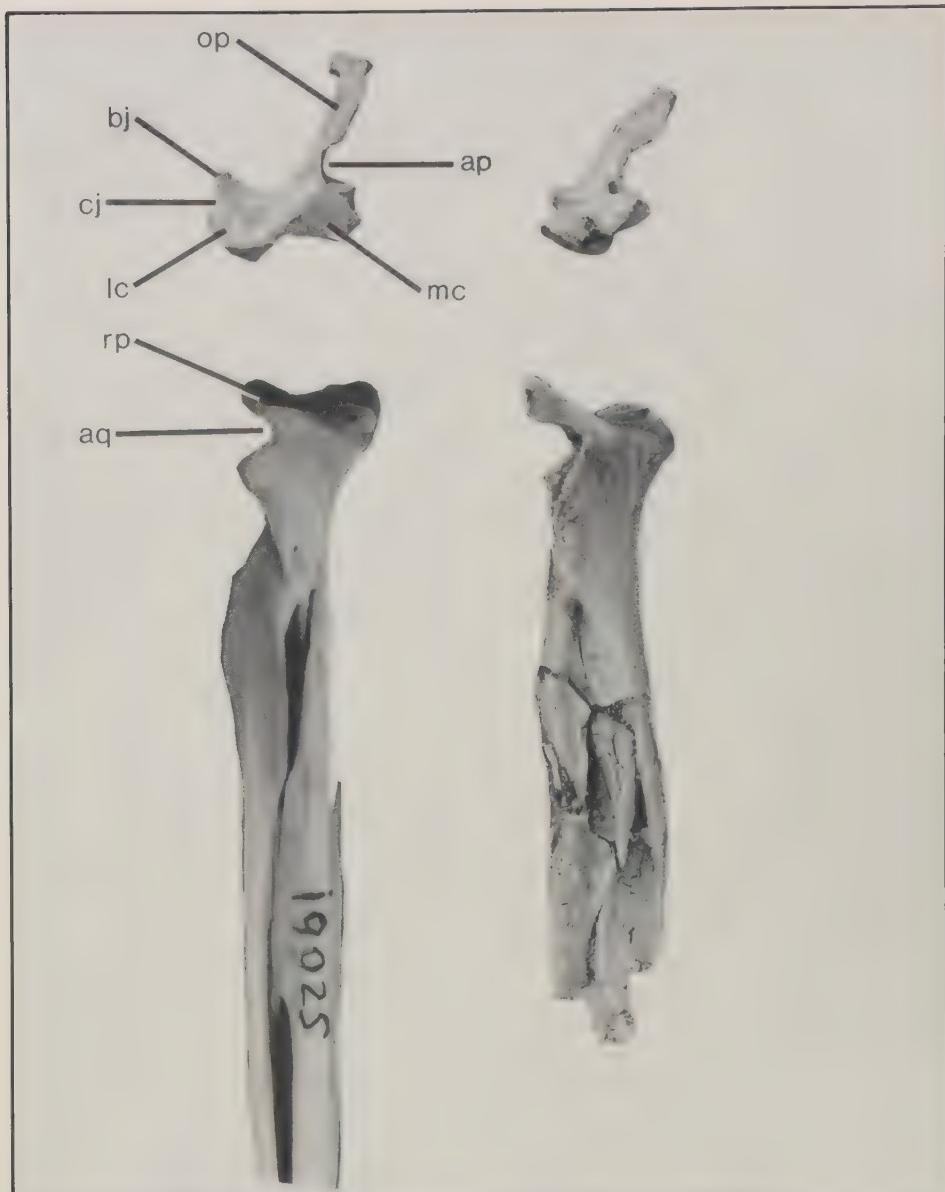
Fig. 8. Quadrates and mandibles of kiwis and lithornithids. Upper left: ventral aspect of right quadrate of *Apteryx australis* (USNM 19025); lower left: left lateral aspect of posterior portion of mandible of *Apteryx australis* (USNM 19025); upper right: ventral aspect of the right quadrate of *Lithornis celetius* (USNM 336200) coated with ammonium chloride; lower right: left lateral aspect of posterior portion of mandible of *Lithornis promiscuus* (holotype USNM 336535) coated with ammonium chloride; all twice natural size. Abbreviations: ap—articulation with pterygoid, aq—notch-like articular fossa for quadrate, bj—buttress for quadratojugal, cj—cotyle for articulation of quadratojugal, lc—lateral mandibular condyle, mc—medial mandibular condyle, op—orbital process, rp—retroarticular process.
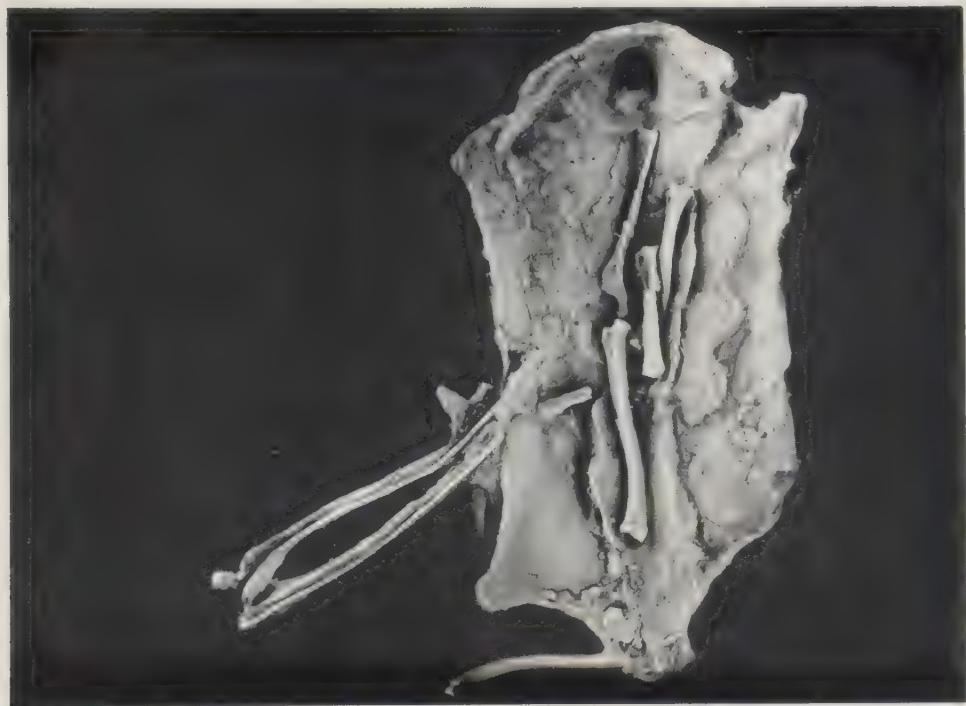
Fig. 9. Dorsal aspect of sternum and ribs of *Lithornis celetius* (PU 16961), natural size, coated with ammonium chloride.
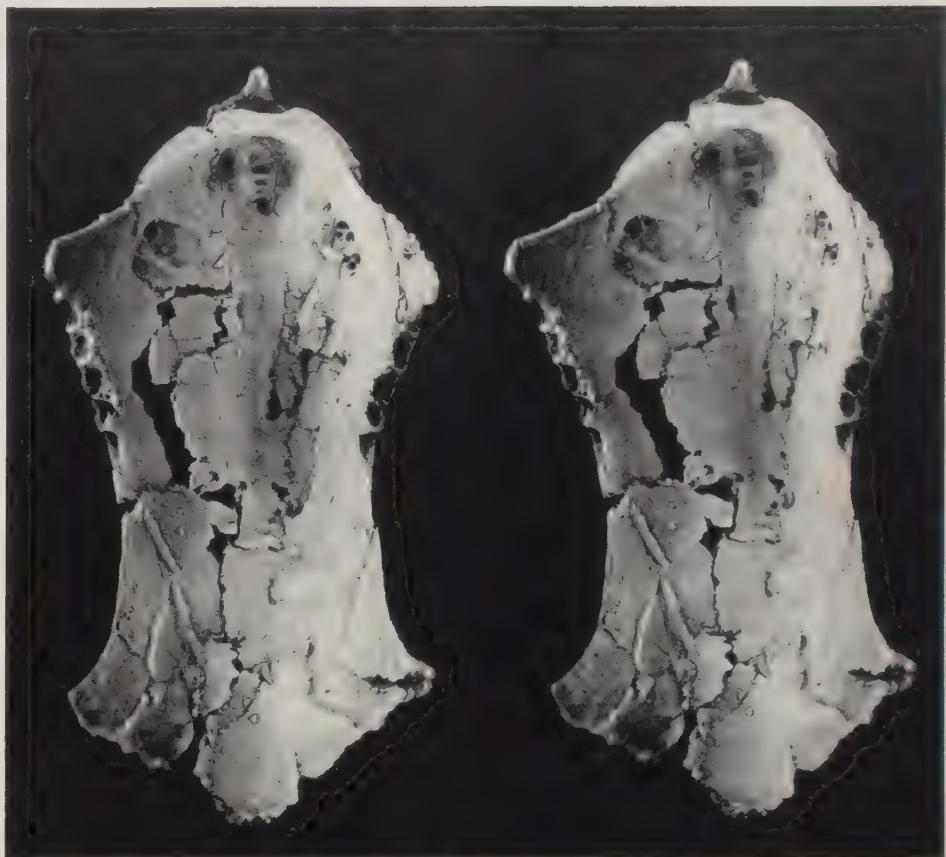
Fig. 10. Stereo image of dorsal aspect of sternum of *Lithornis promiscuus* (holotype USNM 336535), natural size, coated with ammonium chloride.
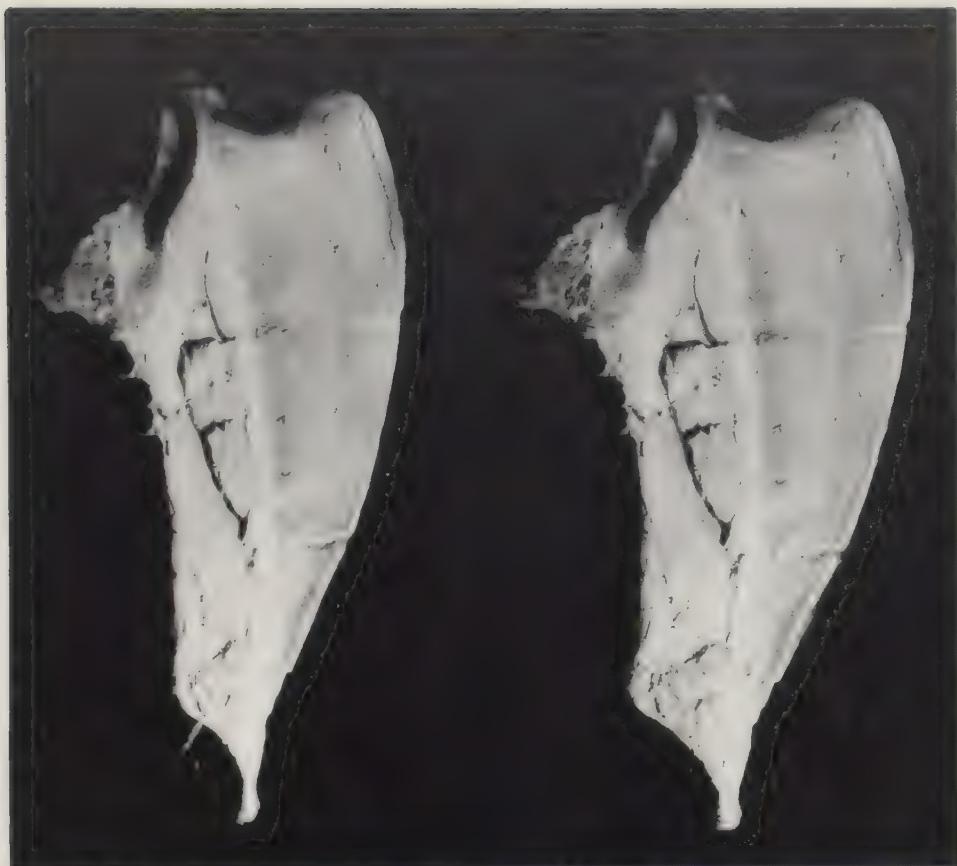
Fig. 11.   Stereo image of right lateral aspect of sternum of *Lithornis promiscuus* (holotype USNM 336535), natural size, coated with ammonium chloride.
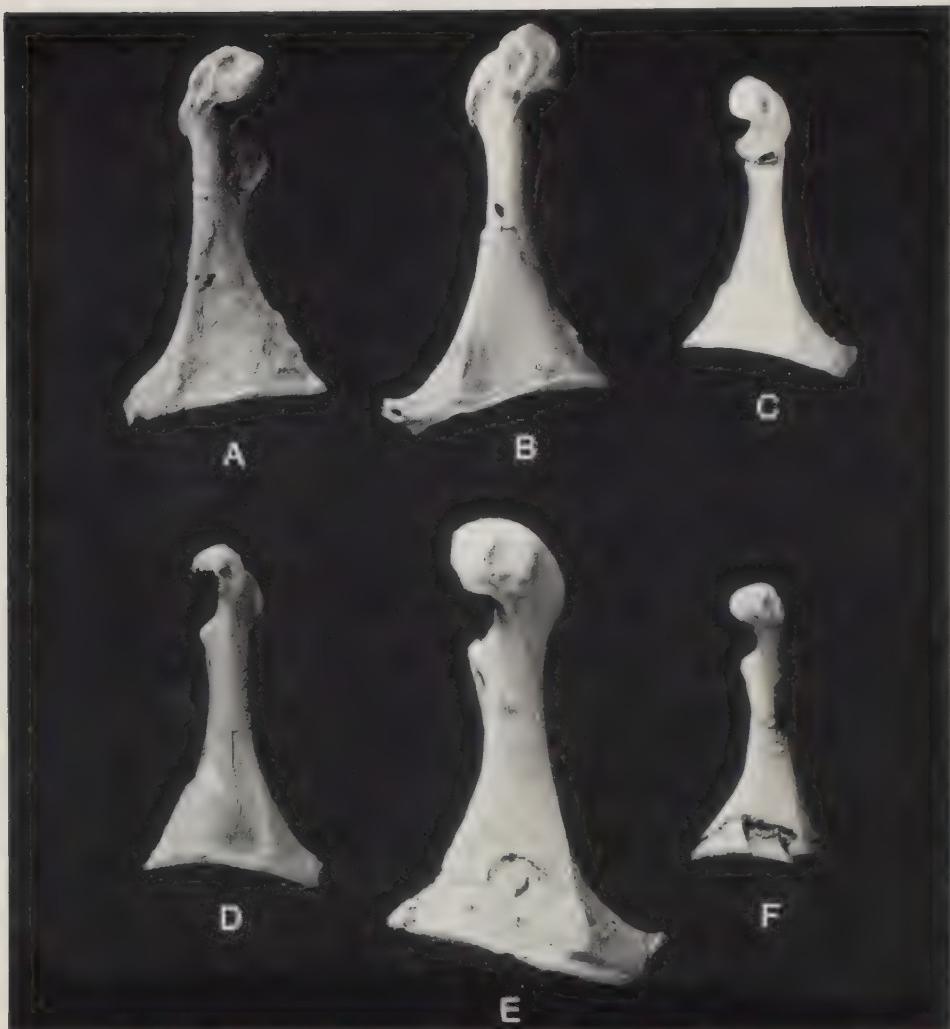
Fig. 12. Ventral aspect of lithornithid coracoids. A. *Lithornis celetius*, right (USNM 290554). B. *Lithornis promiscuus*, right (holotype USNM 336535). C. *Lithornis plebius*, left (holotype USNM 336534). D. cf. *Pseudocrypturus cercanaxius*, left (WN 80280). E. *Paracathartes howardae*, left (USNM 361417). F. Lithornithidae, *incertae sedis* (WN 78210 B). All natural size and coated with ammonium chloride.
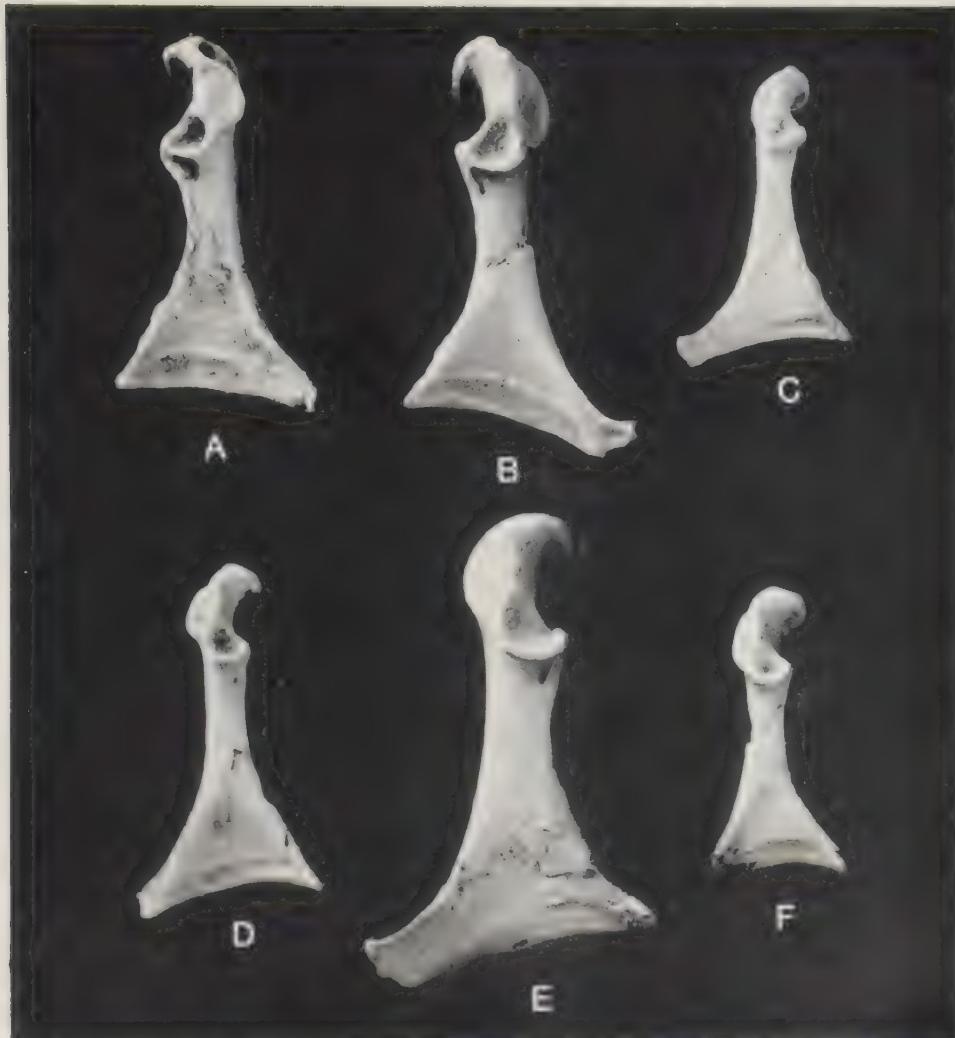
Fig. 13. Dorsal aspect of lithornithid coracoids. A. *Lithornis celetius,* right (USNM 290554). B. *Lithornis promiscuus,* right (holotype USNM 336535). C. *Lithornis plebius,* left (holotype USNM 336534). D. cf. *Pseudocrypturus cercanaxius,* left (WN 80280). E. *Paracathartes howardae,* left (USNM 361417). F. Lithornithidae, *incertae sedis* (WN 78210 B). All natural size and coated with ammonium chloride.

Fig. 14.   Dorsal aspect of lithornithid scapulae. A. *Lithornis celetius*, right (PU 23484). B. *Lithornis celetius*, left (USNM 290554). C. *Lithornis promiscuus*, left (holotype USNM 336535). D. *Lithornis plebius*, right (holotype USNM 336534), E. *Paracathartes howardae*, left (USNM 361419). F. cf. *Pseudocrypturus cercanaxius*, left (WN 80280). G. Lithornithidae, *incertae sedis* (WN 78210 B). All natural size and coated with ammonium chloride. Abbreviation: ac—styloid acromion.
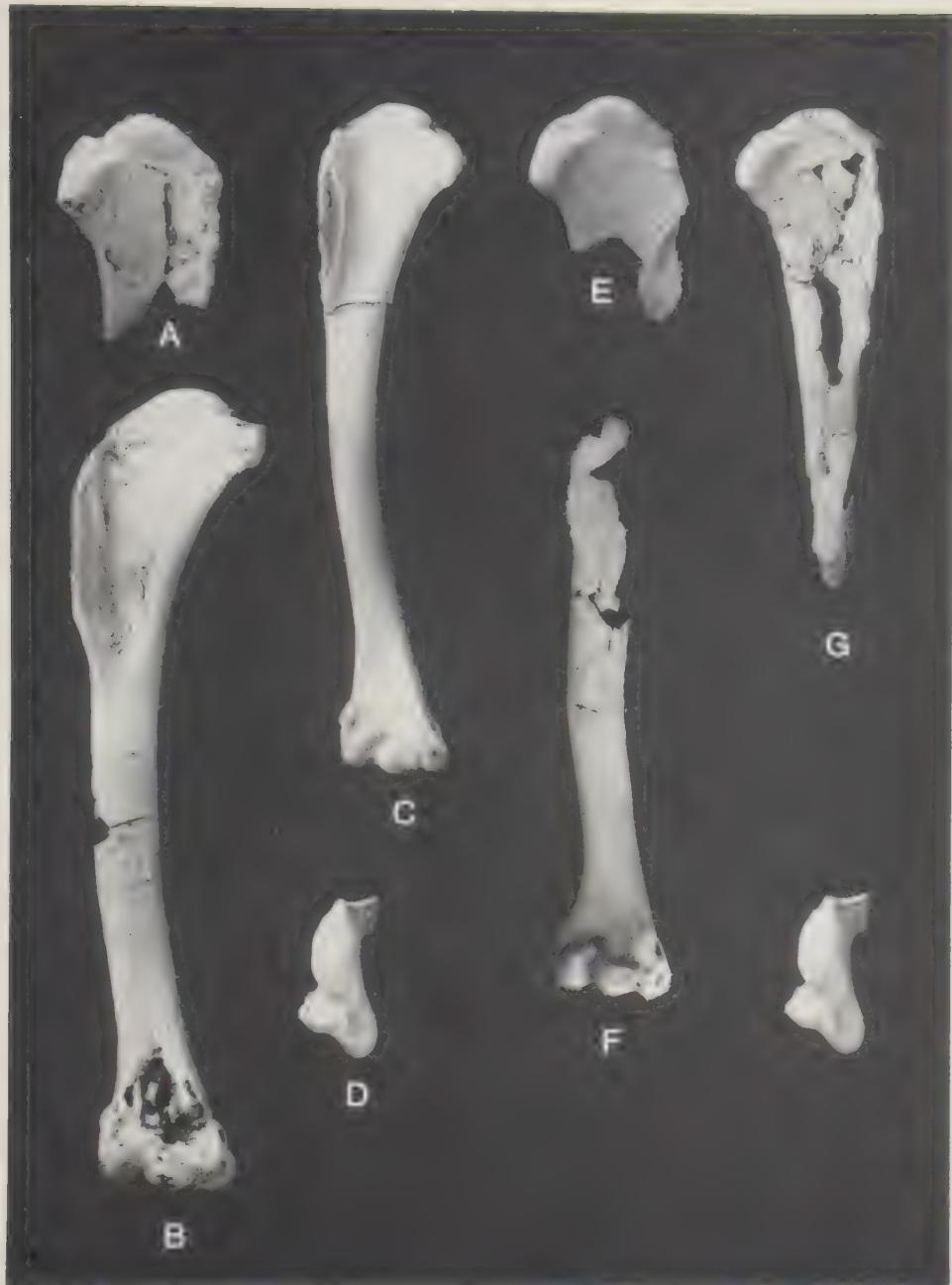
Fig. 15.   Palmar aspect of lithornithid humeri. A. *Lithornis celetius*, proximal left (PU 23483). B. *Lithornis celetius*, right (PU 23485). C. *Lithornis plebius*, right (holotype USNM 336534). D. cf. *Pseudocrypturus cercanaxius*, stereo image of proximal aspect of left (WN 80280). E. cf. *Pseudocrypturus cercanaxius*, proximal left (WN 80280). F. cf. *Pseudocrypturus cercanaxius*, incomplete right (WN 80280). G. Lithornithidae, *incertae sedis*, proximal left (WN 78210 B). All natural size and coated with ammonium chloride.

Fig. 16.   Palmar aspect of lithornithid humeri. A. *Lithornis promiscuus*, left (holotype USNM 336535). B. *Paracathartes howardae*, incomplete right (USNM 361421). C. *Paracathartes howardae*, incomplete right (USNM 361420). All natural size and coated with ammonium chloride.

Fig. 17.　Anconal aspect of lithornithid humeri. A. *Lithornis celetius*, right (PU 23485). B. *Lithornis promiscuus*, left (holotype 336535). C. *Lithornis plebius*, right (holotype USNM 336534). D. *Paracathartes howardae*, incomplete right (USNM 361420). E. *Paracathartes howardae*, incomplete right (USNM 361421). All natural size and coated with ammonium chloride.

Fig. 18. Anterior aspect of lithornithid radii. A. *Lithornis celetius*, distal right (USNM 336200). B. *Lithornis promiscuus*, left (holotype USNM 336535). C. Lithornithidae, *incertae sedis*, left (WN 78210 B). D. cf. *Pseudocrypturus cercanaxius*, distal left (WN 80280). E. *Paracathartes howardae*, distal right (USNM 361441). All natural size and coated with ammonium chloride.

Fig. 19.   Dorsal aspect of lithornithid ulnae. A. *Lithornis promiscuus*, left (holotype USNM 336535). B. *Lithornis plebius*, left (holotype USNM 336534). C. *Paracathartes howardae*, incomplete left (USNM 361426). D. *Paracathartes howardae*, left (USNM 361425). All natural size and coated with ammonium chloride.
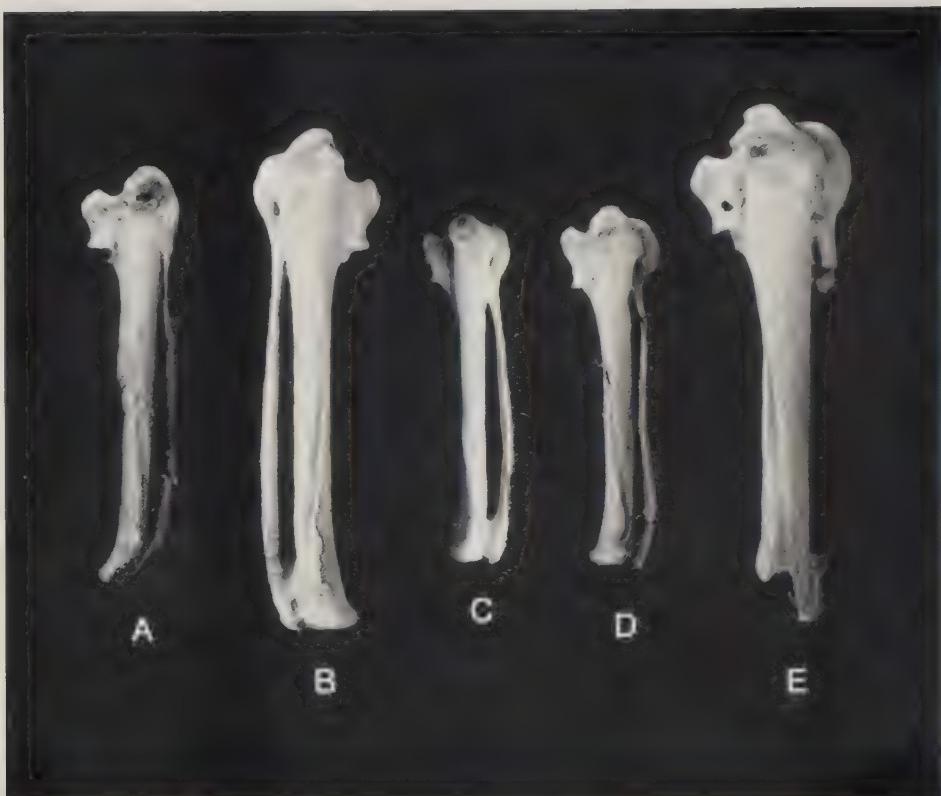
Fig. 20. Dorsal aspect of lithornithid carpometacarpi. A. *Lithornis celetius*, incomplete left (USNM 290554). B. *Lithornis promiscuus*, right (holotype USNM 336535). C. *Lithornis plebius*, left (holotype USNM 336534). D. cf. *Pseudocrypturus cercanaxius*, left (WN 80280). E. *Paracathartes howardae*, incomplete left (USNM 361445). All natural size and coated with ammonium chloride.

Fig. 21.   Lateral aspect of lithornithid pelves. A. *Lithornis celetius,* left preace-
tabular ilium (PU 23485). B. *Lithornis celetius,* incomplete right innominate (holo-
type USNM 290601). C. *Lithornis celetius,* internal aspect of left ischium (holotype
USNM 290601). D. *Lithornis plebius,* incomplete left innominate (holotype USNM
336534). E. *Lithornis promiscuus,* right stereo image (holotype USNM 336535). F.
Lithornis promiscuus, left ischium with apex preserved (holotype USNM 336535).
G. cf. *Pseudocrypturus cercanaxius,* right ischium (WN 80280).
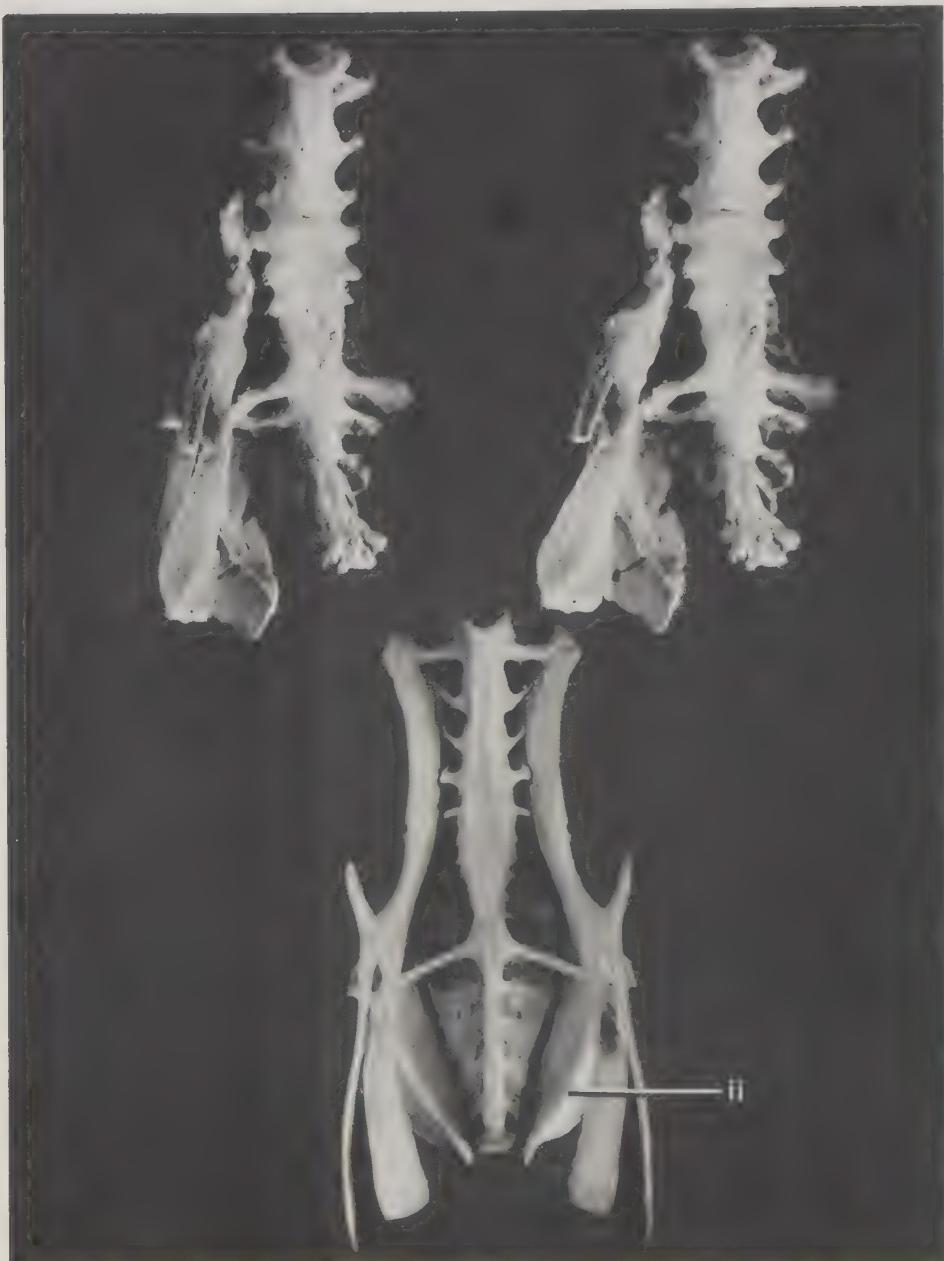
Fig. 22. Ventral aspect of lithornithid and tinamou pelves. Upper stereo image: *Lithornis promiscuus*, lacking left innominate (USNM 336535), coated with ammonium chloride; lower: *Rhynchotus rufescens* (LACM 93347). Note the ridge (ii) for attachment of the ilioischiadic membrane on the ventral surface of the postacetabular ilium, defining the medial extent of the ilioischiadic fossa.

Fig. 23.　Anterior aspect of lithornithid femora. A. *Lithornis celetius*, proximal right (holotype USNM 290601). B. *Lithornis* cf. *nasi*, distal right (UM 73103). C. *Lithornis celetius*, incomplete left (PU 16961). D. *Lithornis promiscuus*, incomplete left (holotype USNM 336535). E. *Lithornis plebius*, left (holotype USNM 336534). F. cf. *Pseudocrypturus cercanaxius*, proximal and distal left ends (WN 80280). G. *Paracathartes howardae*, right (USNM 361412). All natural size and coated with ammonium chloride.
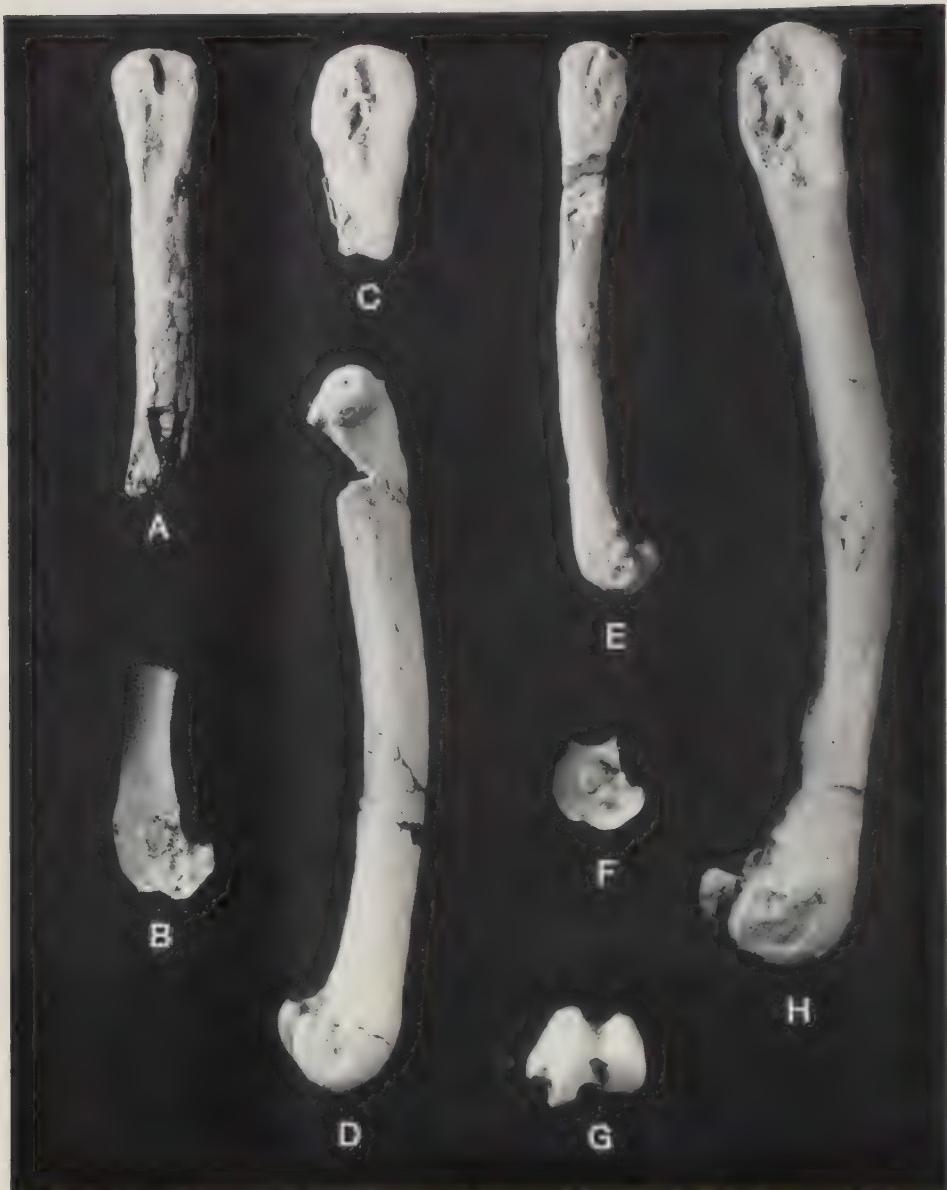
Fig. 24. Lateral aspect of lithornithid femora. A. *Lithornis celetius,* proximal right (holotype USNM 290601). B. *Lithornis celetius,* distal left (PU 16961). C. *Lithornis promiscuus,* proximal right (holotype USNM 336535). D. *Lithornis promiscuus,* medial aspect of incomplete left (holotype USNM 336535). E. *Lithornis plebius,* left (holotype USNM 336534). F. cf. *Pseudocrypturus cercanaxius,* distal left (WN 80280). G. *Lithornis nasi,* distal aspect of right (holotype BMNH A 5200). H. *Paracathartes howardae,* right (USNM 361412). All natural size and coated with ammonium chloride.

Fig. 25. Anterior aspect of lithornithid tibiotarsi. A. *Lithornis promiscuus*, right (holotype USNM 336535). B. *Lithornis plebius*, right (holotype USNM 336534). C. cf. *Pseudocrypturus cercanaxius*, incomplete left (WN 80280). D. *Lithornis nasi*, distal right (holotype BMNH A 5200). E. *?Lithornis hookeri*, distal left (holotype BMNH A 5202). F. *Paracathartes howardae*, right (USNM 361408). All coated with ammonium chloride.
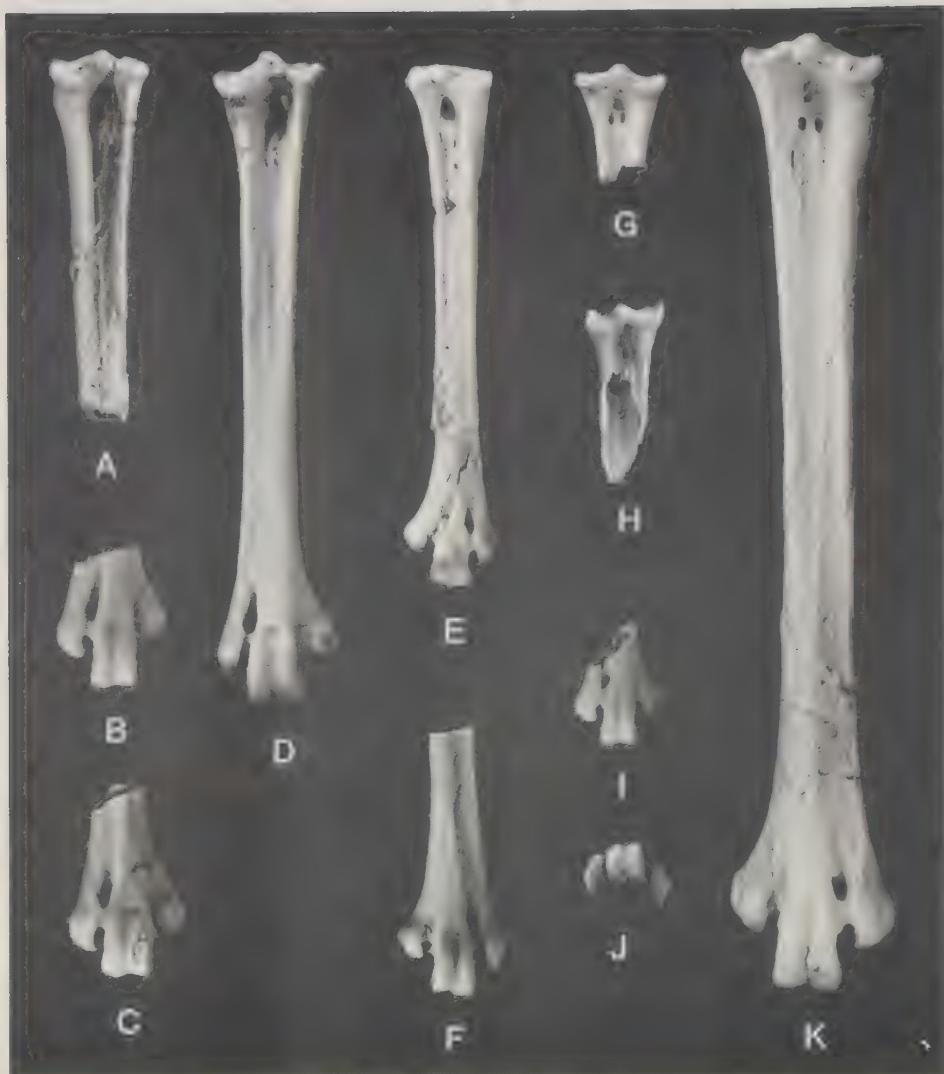
Fig. 26.   Anterior aspect of lithornithid tarsometatarsi. A. *Lithornis celetius*, proximal right (PU 16961). B. *Lithornis celetius*, distal right (PU 23484). C. *Lithornis celetius*, distal right (USNM 290554). D. *Lithornis promiscuus*, right (holotype USNM 336535). E. *Lithornis plebius*, left (holotype USNM 336534). F. *Lithornis* cf. *nasi*, distal left (UM 73103). G. Lithornithidae, *incertae sedis*, proximal left (WN 78210 B). H. cf. *Pseudocrypturus cercanaxius*, proximal right (WN 80280). I. cf. *Pseudocrypturus cercanaxius*, distal right (WN 80280). J. *Pseudocrypturus cercanaxius*, distal aspect of right (WN 80280). K. *Paracathartes howardae*, left (USNM 361406). All natural size and coated with ammonium chloride.
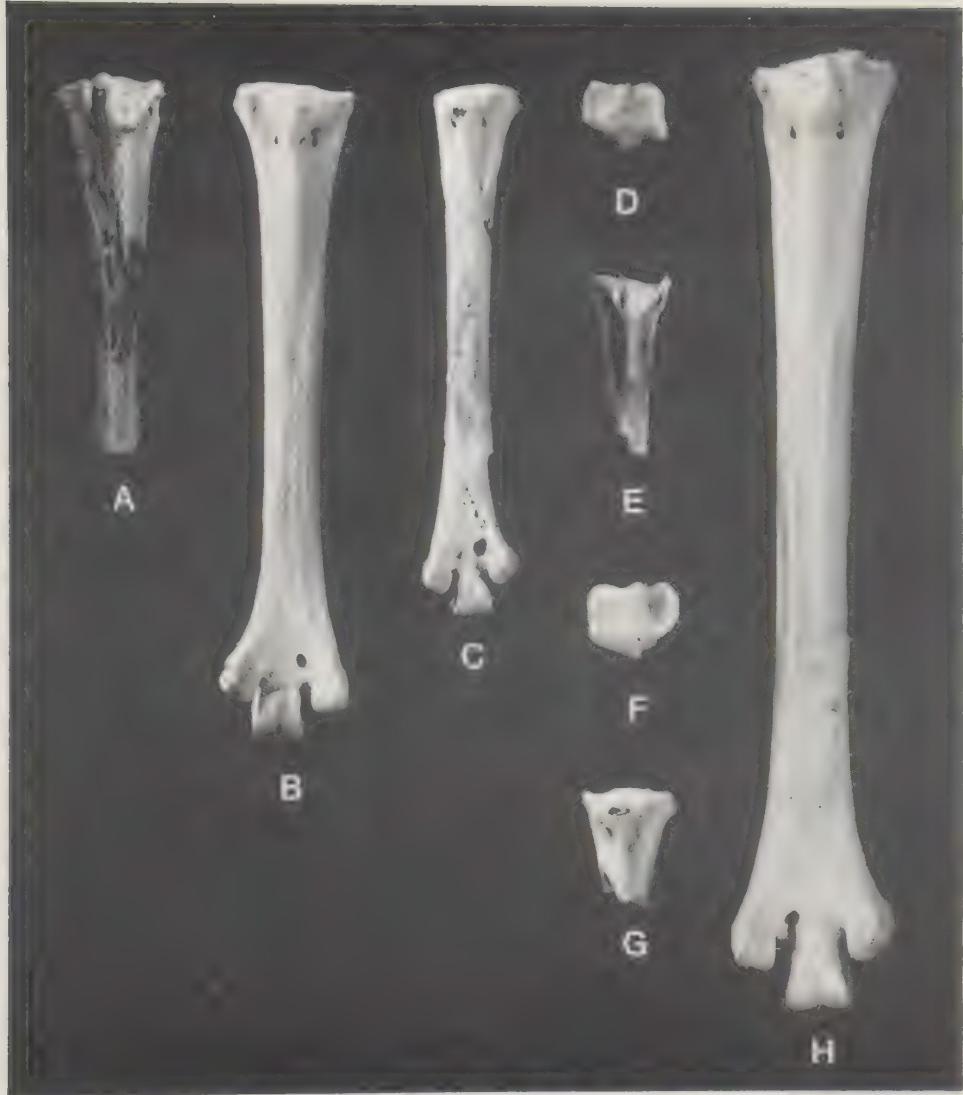
Fig. 27. Posterior aspect of lithornithid tarsometatarsi. A. *Lithornis celetius*, proximal right (PU 16961). B. *Lithornis promiscuus*, right (holotype USNM 336535). C. *Lithornis plebius*, left (holotype USNM 336534). D. cf. *Pseudocrypturus cercanaxius*, proximal aspect of right (WN 80280). E. cf. *Pseudocrypturus cercanaxius*, proximal right (WN 80280). F. Lithornithidae, *incertae sedis*, proximal aspect of left (WN 78210 B). G. Lithornithidae, *incertae sedis*, proximal left (WN 78210 B). H. *Paracathartes howardae*, left (USNM 361406) All natural size and coated with ammonium chloride.

Fig. 28.   Low magnification bright field photomicrographs of the compacta of the tibiotarsi of a tinamou (*Rhynchotus,* PU 728), a ratite (*Casuarius,* USNM 429823), *Lithornis* (USNM 290554), and *Paracathartes* (USNM 361407). All sections are transverse through the distal diaphysis or metaphysis. Vascular canals appear as dark lines, spots, or circles on a light background of bone. Large dark regions are more opaque regions of bone, in which vascular canals may appear as light spots. Scale 0.3 mm.
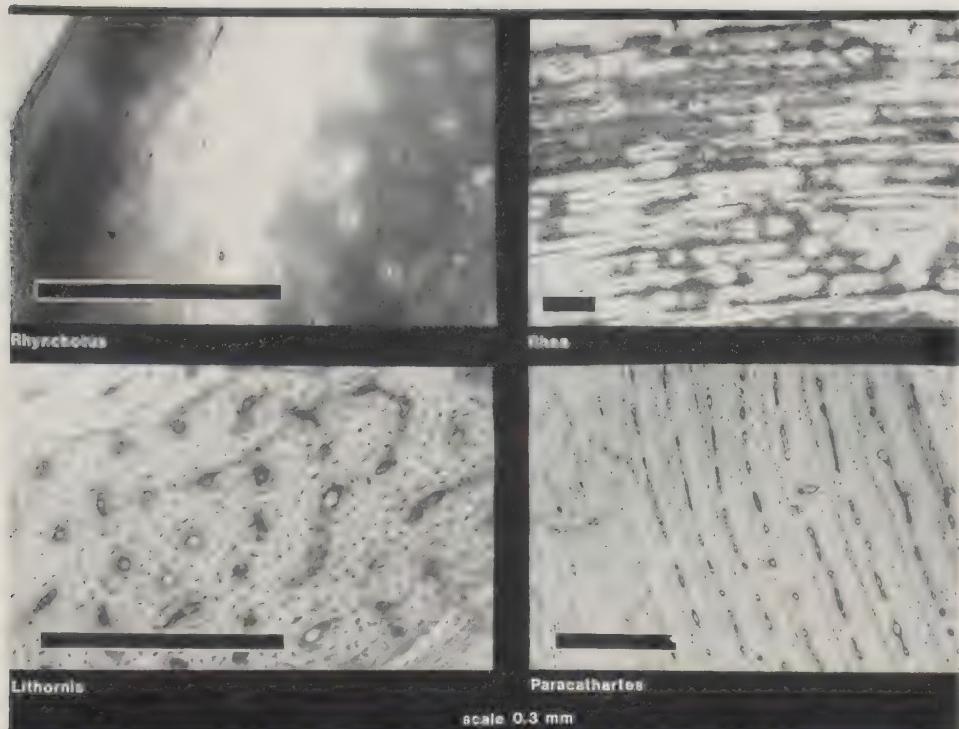
Fig. 29.   Intermediate magnification bright field photomicrographs of the compacta of the tibiotarsi of a tinamou (*Rhynchotus,* PU 728), a ratite (*Rhea,* unnumbered), *Lithornis* (USNM 290554), and *Paracathartes* (USNM 361407). All sections are transverse through the distal diaphysis or metaphysis. Vascular canals appear as dark lines, spots, or circles on a light background of bone. Large dark regions are more opaque regions of bone, in which vascular canals may appear as light spots. Scale 0.3 mm.
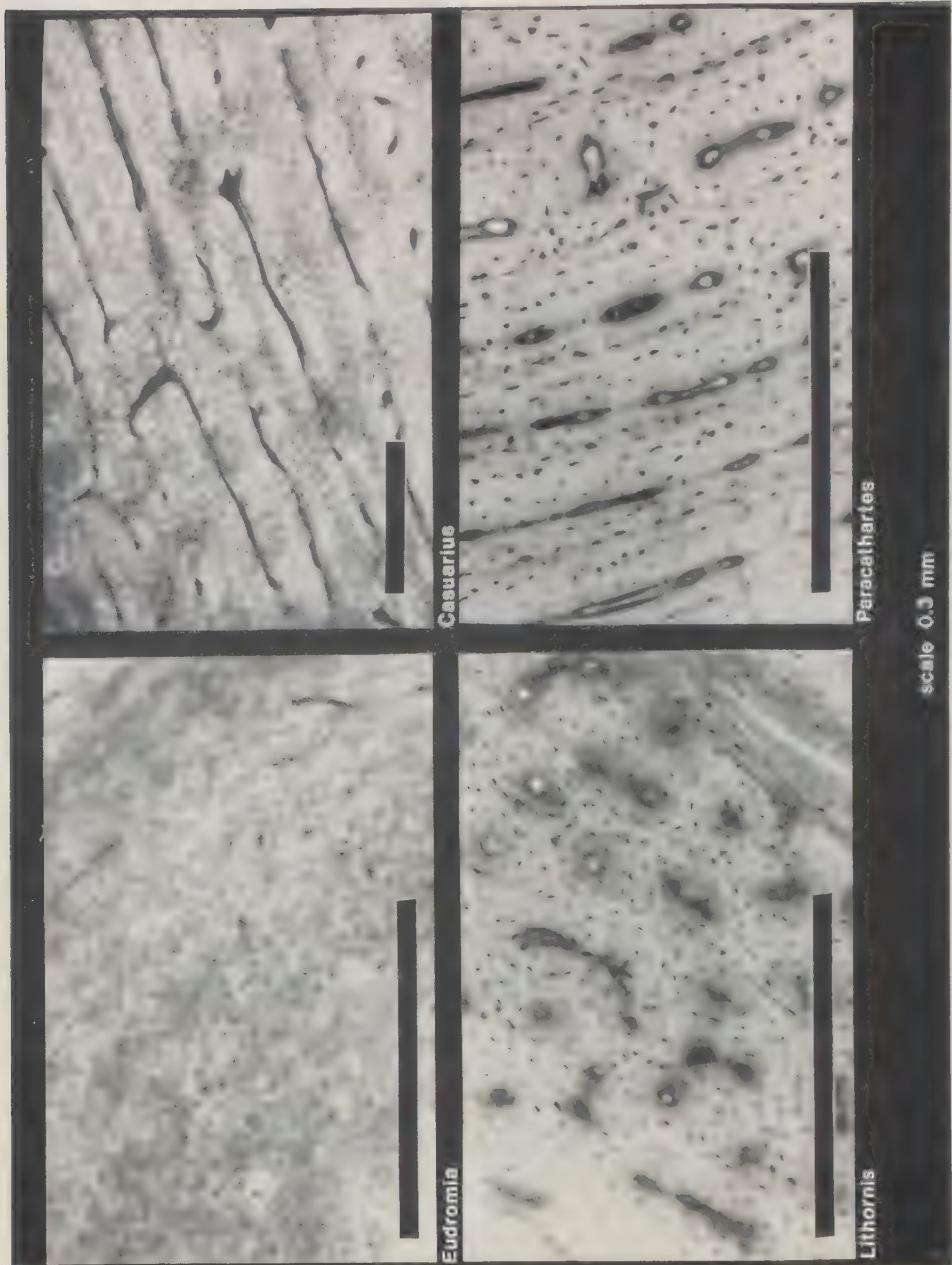
Fig. 30. High magnification bright field photomicrographs of the compacta of the tibiotarsi of a tinamou (*Eudromia*, USNM 345016), a ratite (*Casuarius*, USNM 429823), *Lithornis* (USNM 290554), and *Paracathartes* (USNM 361407). All sections are transverse through the distal diaphysis or metaphysis. Vascular canals appear as dark lines, spots, or circles on a light background of bone. Large dark regions are more opaque regions of bone, in which vascular canals may appear as light spots. Scale 0.3 mm.
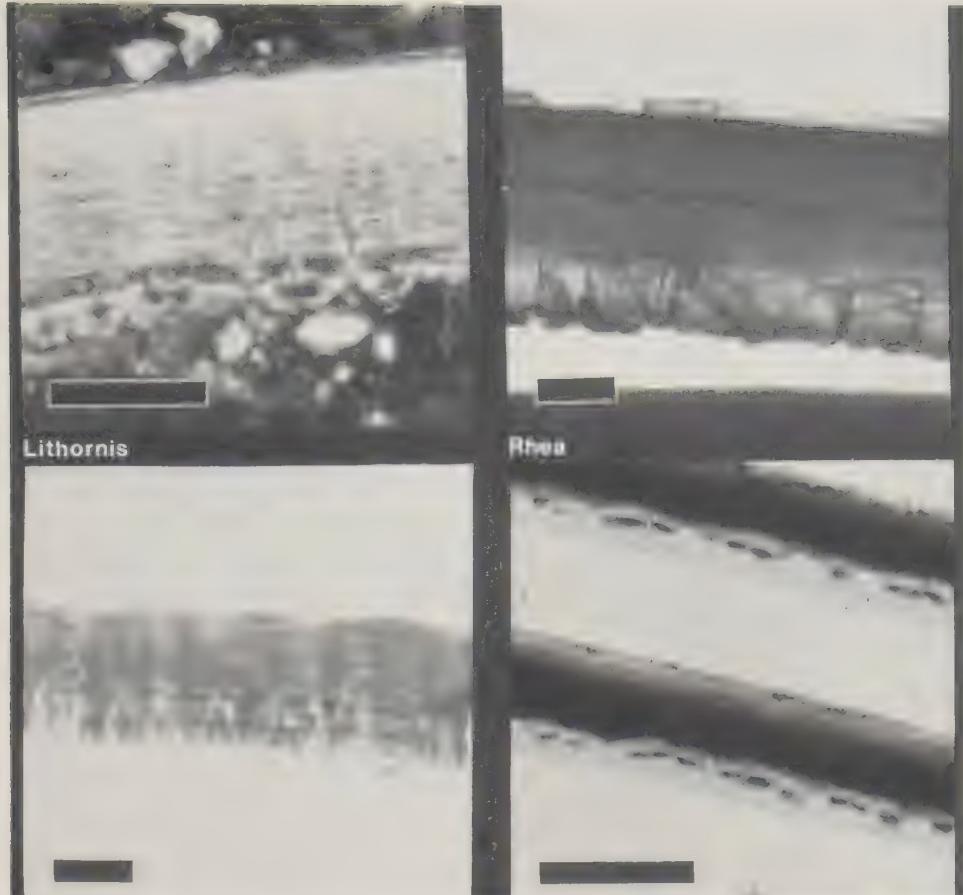
Fig. 31. Radial lapidary thin sections of the eggshells of *Lithornis* (PU 16961), a ratite (*Rhea*), a neognathous outgroup (Galliformes: *Crax*), and a tinamou (*Nothoprocta*). Note the outer (upper) "cuticular layer" in each of the paleognathous birds, but not in the neognathous bird. Also note the inner band that lies adjacent to the mamillary processes in *Lithornis* (dark band) and *Nothoprocta* (light band). Scale 0.3 mm.

Fig. 32.   Holotype of *Lithornis vulturinus*, destroyed in the bombing of London. Lithograph reproduced from Owen (1846, fig. 232).
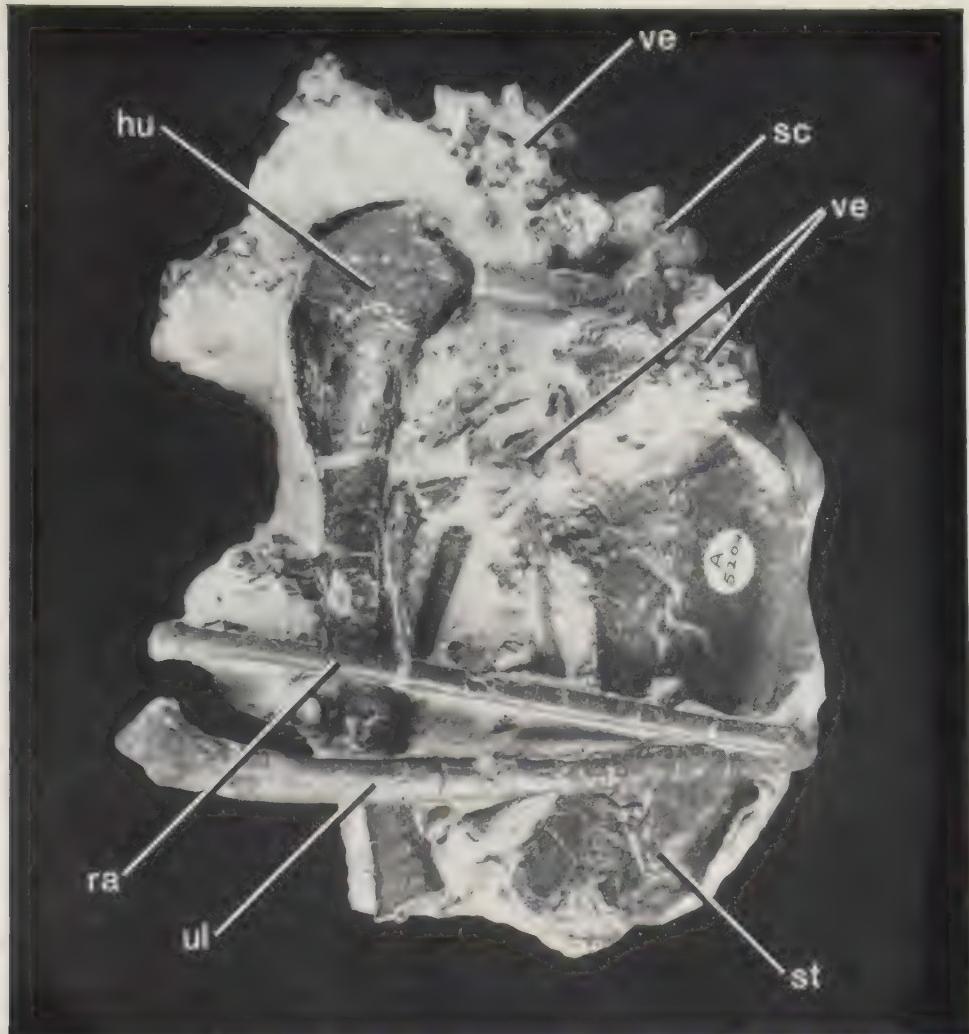
Fig. 33.   Newly designated neotype specimen of *Lithornis vulturinus* (BMNH A 5204) preserved in a pyritic clay nodule. Abbreviations: hu—humerus, ra—radius, sc—scapula, st—sterum, ul—ulna, ve—vertebrae.

Fig. 34.   Crushed articulated skeleton of *Pseudocrypturus ceranaxius*. Privately owned by Siber and Siber.
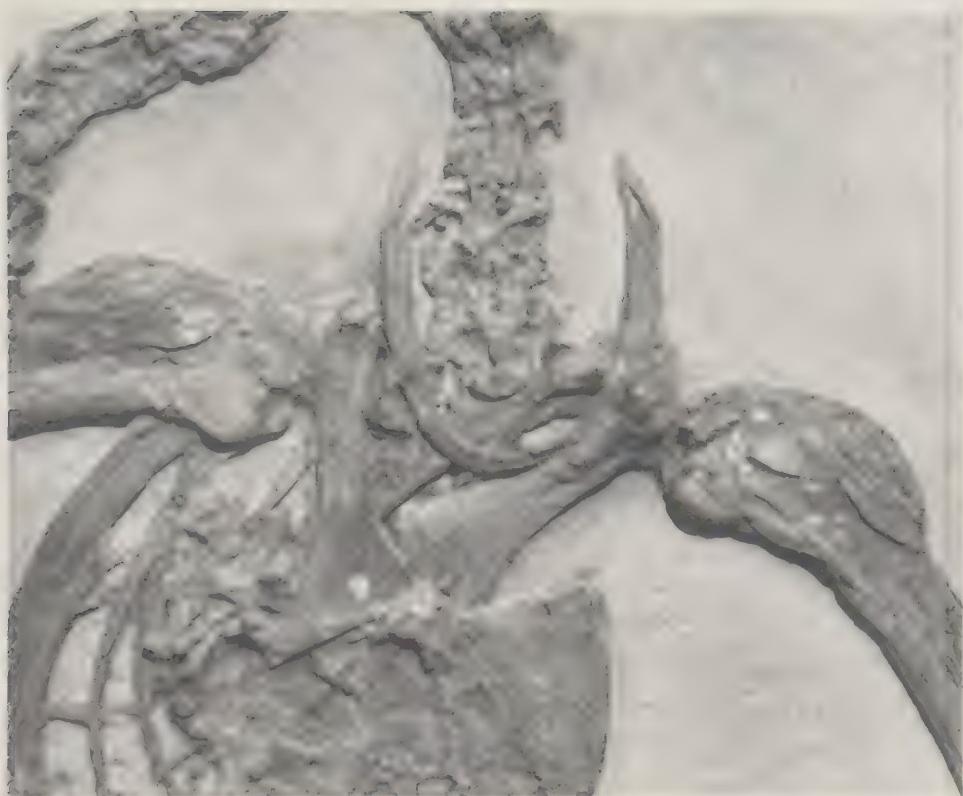
Fig. 35.   Enlargement of furcula and coracoids of crushed articulated skeleton of *Pseudocrypturus cercanaxius*. Privately owned by Siber and Siber.

TABLE 3.   Measurements of lithornithid skulls. Bill and cranium length are measured from the posterior angle of the narial cavity. Specimens UM 73103, BMNH A 5424, and USNM 361415 are only tentatively referred to the taxa listed here.

Specimen	Length	Bill Length	Cranium Length	Bizygomatic Width	Supra-orbital Width	Prefrontal Width
cf. *Lithornis nasi*						
UM 73103	—	—	—	26.9	—	—
Lithornis celetius						
USNM 290601	—	—	—	23.3	7.7	18.7
Lithornis promiscuus						
USNM 391983	96.9	54.5	45.0	23.6	~10.8	—
AMNH 21901	>94.1	56.2	>39.2	—	12.1	—
AMNH 21900	—	—	—	—	12.0	21.3
Lithornis plebius						
USNM 336534	—	—	—	23.6	8.8	—
Pseudocrypturus cercanaxius						
USNM 336103	95.6	51.9	43.9	—	—	—
Siber specimen	96.2	53.5	44.2	—	—	—
BMNH A 5424	—	—	—	>24.2	—	—
Paracathartes howardae						
USNM 404758	—	71.5	—	>25.8	—	—
USNM 361415	—	—	—	—	—	—

SYSTEMATIC PALEONTOLOGY

TABLE 4. Measurements of lithornithid vertebrae. "Length" is measured from anterior to posterior zygapophyses, except for the pygostyle, which is total length. Length of the vertebral body of C2 includes the odontoid process. "Width" measurements preceded by "~" are estimated by doubling unilateral measurements. Lithornithids possess 15 cervical and 8 thoracic vertebrae, based on the Siber specimen of *Pseudocrypturus cercanaxius*, the only species for which all the presacral vertebrae are known. Specimen UM 73103 is only tentatively referred to *Lithornis nasi*. C = cervical, T = thoracic, Cc = caudal, Ps = pygostyle, (i), (j) = unknown vertebral levels.

Specimen	Vertebral Level	Length	Length Body	Maximum Width
Lithornis vulturinus				
BMNH A 5204	C9	~14.8	~11.8	——
BMNH A 5204	C10	14.1	12.3	——
BMNH A 5204	C12	14.1	——	12.7
BMNH A 5204	C13	12.2	10.7	——
BMNH A 5204	C15	——	9.3	~13.6
BMNH A 5204	T1	——	9.0	~16.6
Lithornis nasi				
BMNH A 5455	C2	——	——	~10.4
BMNH A 5455	C3	8.4	7.3	~ 9.4
BMNH A 5455	C4	10.7	8.6	8.6
BMNH A 5455	C5	——	10.3	——
BMNH A 5455	C10	13.5	11.3	11.8
BMNH A 5455	T1	——	10.2	——
BMNH A 5455	T4	——	11.1	——
BMNH A 5455	T5	——	10.8	——
BMNH A 5200	T6	——	11.5	——
UM 73103	T6	13.6	11.5	——
BMNH A 5200	T7	12.9	10.8	——
UM 73103	T7	13.1	——	——
Lithornis celetius				
PU 23483	C2	9.0	7.8	~ 9.7
PU 16961	C4	11.4	9.5	10.8
PU 23483	C4	9.7	9.1	~ 8.4
PU 16961	C5	8.3	11.1	10.9
PU 23483	C5	——	11.7	~ 9.3
PU 23483	C7	15.1	12.7	11.5
PU 23483	C8	15.3	13.3	11.8
PU 23483	C9	14.9	12.2	——
PU 16961	C10	14.7	13.4	~13.0
PU 23483	C10	14.2	12.3	12.0
PU 23483	C11	14.3	12.6	12.6
PU 23483	C12	13.9	12.4	12.9
PU 23483	C13	14.2	11.7	13.5
PU 16961	T1	——	8.8	——

TABLE 4 (Continued)

USNM 290554	T4	14.6	11.4	~20.6
USNM 290554	T8	13.3	11.7	21.1
USNM 290601	Ccl	——	3.2	5.2
Lithornis promiscuus				
USNM 336535	C1	——	1.7	6.8
USNM 336535	C2	10.9	9.8	10.8
AMNH 21900	C2	9.2	——	9.7
UM 69343	C2	8.4	10.3	9.8
USNM 336535	C4	>13.0	11.6	10.8
USNM 336535	C5	17.5	13.2	11.7
USNM 336535	C6	18.7	13.5	13.0
USNM 391983	C6	19.1	11.1	12.7
USNM 391983	C7	18.5	——	12.4
USNM 336535	C8	17.8	——	——
UM 69343	C10	16.7	14.4	11.5
UM 69343	C11	16.8	14.4	12.9
UM 69343	C12	16.1	——	13.4
UM 69343	C14	16.1	11.8	14.5
USNM 336535	C15	——	10.9	16.3
USNM 336535	T1	15.6	10.1	17.3
USNM 336535	T3	16.1	12.7	17.8
USNM 391983	T3	16.2	13.9	——
AMNH 21900	T3	14.8	13.9	16.7
AMNH 21900	T4	17.4	15.5	~19.8
USNM 336535	T5	17.0	14.5	~19.6
USNM 336535	T6	——	——	20.9
AMNH 21900	T6	16.3	14.4	~21.4
USNM 336535	T7	15.5	12.0	23.1
USNM 391983	T7	16.7	15.1	——
AMNH 21900	T7	17.9	13.4	~22.6
AMNH 21900	T8	15.5	——	——
USNM 336535	Ss	>74.4	——	~28.4
AMNH 21900	Ss	>75.4	——	——
USNM 336535	Ccl	——	4.2	5.6
USNM 336535	Ps	11.6	9.7	2.9
Lithornis plebius				
USNM 336534	C2	6.5	——	9.7
USNM 336534	C8	12.6	10.6	10.6
USNM 336534	C9	12.2	10.3	11.0
USNM 336534	C10	12.4	10.6	~11.8
USNM 336534	C14	11.3	8.8	11.7
USNM 336534	C15	11.6	7.7	12.3
USNM 336534	T4	12.6	10.0	13.5
USNM 336534	T5	12.2	~11.3	14.0
USNM 336534	T6	11.7	9.8	14.9
USNM 336534	T8	——	9.4	~17.4
USNM 336534	Ps	10.3	7.3	1.7

Pseudocrypturus cercanaxius

Siber specimen	C1	——	——	8.6
USNM 336103	C2	7.7	——	——
Siber specimen	C2	7.8	~ 8.2	8.7
USNM 336103	C3	10.2	——	——
Siber specimen	C3	9.3	——	——
USNM 336103	C4	11.5	——	——
Siber specimen	C4	10.0	——	——
USNM 336103	C5	~15.8	——	——
Siber specimen	C5	12.8	——	——
USMN 336103	C6	15.9	——	——
Siber specimen	C6	15.5	——	——
USNM 336103	C7	13.8	——	——
Siber specimen	C7	13.8	——	——
USNM 336103	C8	14.5	——	——
Siber specimen	C8	14.0	——	——
Siber specimen	C9	13.3	11.2	——
Siber specimen	C10	12.2	10.8	——
Siber specimen	C11	12.4	10.8	——
Siber specimen	C12	11.6	10.0	——
Siber specimen	C13	12.6	10.0	——
Siber specimen	C14	12.0	9.2	——
Siber specimen	C15	——	8.2	——
Siber specimen	T1	——	8.1	——
Siber specimen	T4	——	11.7	——
Siber specimen	T6	——	11.0	——
Siber specimen	T7	——	10.4	——
Siber specimen	T8	——	10.8	——

Paracathartes howardae

USNM 404756	C2	10.1	12.2	12.3
USNM 361428	C3	11.8	9.6	12.7
USNM 361429	C3	13.1	10.9	12.9
USNM 361430	C5	20.4	15.2	12.4
USNM 404754	C6	21.7	17.0	>12.8
USNM 361431	C7	19.5	17.2	>13.8
USNM 404751	C7	19.6	17.2	>13.4
USNM 404757	C8	20.2	——	>15.2
USNM 361432	C9	~18.4	17.2	——
USNM 404753	C9	19.7	17.1	>14.1
USNM 361434	C10	19.2	17.0	17.0
USNM 361433	C11	19.2	16.9	>15.8
USNM 404752	C12	19.3	15.9	>15.3
USNM 404755	T1	——	10.7	>16.1
USNM 361436	Cc(i)	——	3.5	4.9
USNM 361436	Cc(j)	——	3.5	~6.4
USNM 361436	Cc(j+1)	——	3.6	6.2
USNM 361436	Cc(j+2)	——	3.3	6.0
USNM 361435	Ps	17.0	14.1	3.0

TABLE 5. Measurements of lithornithid sterna. Specimen WN 80280 is only tentatively referred to *Pseudocrypturus cercanaxius*.

Specimen	Length (from Manubrium)	Maximum Width (at sterno= coracoid)	Minimum Width (posterior to costal margin)	Carina Depth (approx.)
Lithornis vulturinus BMNH 38935	——	——	33.0	——
Lithornis celetius PU 16961	>75.0	~41.0	31.6	19
Lithornis promiscuus USNM 336535	90.0	42.5	28.4	21
Pseudocrypturus cercanaxius Siber specimen	77.2	——	——	20
WN 80280	——	——	——	21

TABLE 6. Measurements of lithornithid furculae.

Specimen	Dorso-ventral Length	Width at Dorsal Extremity
Lithornis promiscuus USNM 336535	40.7	35.8
Pseudocrypturus cercanaxius Siber specimen	37.0	36.0

TABLE 7. Measurements of lithornithid coracoids. Specimens BMNH A 5303 and WN 80280 are only tentatively referred to the taxa listed here.

Specimen	Length	Medial to Lateral Angle	Sternal Articulation to Scapular Cotyla	Minimum Width Neck
Lithornis nasi BMNH A 5455	——	——	25.0	5.0
WN 74067	36.1	>>21.1	25.5	5.3
WN 79238	>>34.2	>20.3	23.9	4.2
Lithornis promiscuus USNM 336535	42.7/42.7	27.0(r)	28.7/29.0	6.7/6.7
AMNH 21900	>40.5	——	~27.7	6.1
UM 69343	>40.1(1)	26.5(1)	27.9(1)	6.5(1)

Lithornis plebius

USNM 336534	~31.1(1)	20.7(1)	22.9(1)	4.1(1)
AMNH 21902	——	>19.4	——	——
BMNH A 5303	30.9	20.1	22.3	4.3

Pseudocrypturus cercanaxius

Siber specimen	35.6/36.8	~21(r)	——	——
WN 80280	36.1(1)	21.0(1)	26.0(1)	4.5(1)

Paracathartes howardae

USNM 361416	53.7	34.5	38.0	8.4
USNM 361417	50.0	32.3	34.2	7.9

TABLE 8.   Measurements of lithornithid coracoids. Specimens BMNH A 5303 and WN 80280 are only tentatively referred to the taxa listed here.

Specimen	Procoracoid Length	Dorso-Ventral Width Acrocoracoid	Glenoid Width	Scapular Cotyla Diameter
Lithornis nasi				
BMNH A 5455	——	——	5.2	4.6
WN 74067	7.3	——	——	——
WN 79238	6.5	——	——	——
Lithornis celetius				
USNM 290554	<8.6	8.0	6.0	——
Lithornis promiscuus				
USNM 336535	9.1/9.2	10.0/10.0	7.1/7.1	6.4/6.3
AMNH 21900	~8.8	——	6.8	~5.0
UM 69343	9.0(1)	>8.4(1)	6.6(r)	5.7(1)
Lithornis plebius				
USNM 336534	>6.0(1)	6.0(1)	4.2(1)	~3.2(1)
BMNH A 5303	~6.0	6.5	4.6	——
Pseudocrypturus cercanaxius				
Siber specimen	——	6.6(1)	——	——
WN 80280	6.5(1)	~6.3(1)	4.9(1)	4.0(1)
Paracathartes howardae				
USNM 361416	11.0	11.0	8.3	6.4
USNM 361417	11.1	10.9	7.7	7.2

TABLE 9. Measurements of lithornithid scapulae. "Width" of the neck and body and "breadth" of the head of the acromion are measured dorsoventrally. Specimen BMNH A 5303 is only tentatively referred to *Lithornis plebius*.

Specimen	Total Length	Length from Coracoid Cotyla	Neck Width	Body Width	Length Glenoid	Width Glenoid Facet	Breadth Acromion to Glenoid
Lithornis vulturinus							
BMNH A 5204	—	~65.0	~6.2	—	9.5	5.8	11.2
Lithornis nasi							
BMNH A 5455	—		5.3(r)	5.2(1)	~8.9/9.1	—	—
WN 83445	—	>59.5				—	—
Lithornis celetius							
USNM 290554	>>53.9	>>46.7	~6.0	~6.3	9.2	5.5	~12.1
PU 23484	—	>61.1	5.6	5.8	8.4	—	—
Lithornis promiscuus							
USNM 336535	81.3(1)	74.7(1)	6.8/6.8	7.1/6.9	11.5/11.6	6.0/6.0	12.9/12.8
UM 69343(1)	—	—	6.5	6.4	10.6	6.6	12.0
Lithornis plebius							
USNM 336534	>57.1(r)	>51.8(r)	4.3/4.4	4.3/4.6	8.0/8.3	3.8/3.8	9.0/9.2
BMNH A 5303	—	—	4.5	4.4	—	4.5	9.4
Pseudocrypturus cercanaxius							
Siber specimen (r)	63.7	57.2	—	5.6	—	—	—
Paracathartes howardae							
USNM 361418	—	79.9	9.8	11.8	~14.0	—	—
USNM 361419	>>85	>>74.3	10.0	11.7	13.5	8.2	17.4

TABLE 10. Measurements of lithornithid humeri. Specimens BMNH A 5303 and WN 80280 are only tentatively referred to the taxa listed here.

Specimen	Length	Distal Pectoral Crest to Capitulum	Width Caput	Dorsal Tubercle to Post. Bicipital Crest	Length Caput to Dist. Pectoral Crest
Lithornis vulturinus					
BMNH A 5201	>>91.3	—		21.6	38.7
BMNH 33138	—	—	7.0	22.4	40.1
Lithornis nasi					
BMNH A 5200	—	—	5.9		—
BMNH A 5455(1)	—	—	6.2	20.1	—
Lithornis celetius					
USNM 290554	—	—	6.3		
PU 23483	—	—	>5.7	19.8	
PU 23884	96.7	~66.1	>5.7		~31.8
PU 23485	—	—	6.2	20.7	34.7
Lithornis promiscuus					
USNM 336535(1)	112.7	~75.5	7.5	26.3	~42.7
Lithornis plebius					
USNM 336534	78.2	54.7	5.3	16.9	27.5
AMNH 21902	83.5	56.3	5.0	17.5	30.0
BMNH A 5303	81.6	56.1	4.7	16.3	28.2

Continued

TABLE 10 (Continued)

Specimen	Length Internal Tuberosity (from Coraco-Brachial Region)	Width Distal Condyles	Width Capitulum (Palmar-anconical)	Maximum Midshaft Diameter	Minimum Midshaft Diameter
Pseudocrypturus cercanaxius Siber specimen WN 80280	~84.4 / —	~53.8 / 53.7(1)	5.2(r)	~18.2 / 18.3(r)	~29.2 / —
Paracathartes howardae USNM 361420	>123.6	80.7	8.8	31.6	44.1
USNM 361421	—	—	—	—	—

TABLE 11. Measurements of lithornithid humeri. Specimens BMNH A 4490, BMNH A 5303, and WN 80280 are only tentatively referred to the taxa listed here.

Specimen	Length Internal Tuberosity (from Coraco-Brachial Region)	Width Distal Condyles	Width Capitulum (Palmar-anconical)	Maximum Midshaft Diameter	Minimum Midshaft Diameter
Lithornis vulturinus					
BMNH A 5204	—	—	—	7.3	
BMNH 33138	—	—	—	~8.2	6.8
Lithornis nasi					
BMNH A 5455	9.9(1)	14.9/15.1	8.5/8.5	7.2(1)	6.1(1)
WN 79238	—	13.6	—	—	
MMH.V.P. 1285 A	—	>14.7	8.6	7.0	5.4

?Lithornis hookeri					
BMNH A 3769	—	10.3	6.1	~5.1	~4.0
Lithornis celetius					
USNM 290554	10.1	—	—	—	—
PU 23483	9.6	—	—	7.0	6.2
PU 23484	—	—	>8.5	7.0	6.2
PU 23485	—	16.2	8.9	7.6	5.4
Lithornis promiscuus					
USNM 336535	11.8(1)	20.1(1)	10.9/10.7	9.7(1)	8.2(1)
UM 69343	—	—	—	8.5	6.6
Lithornis plebius					
USNM 336534	7.3	12.5	7.2	5.5	4.7
AMNH 21902	7.8	12.8	7.2	5.7	4.7
BMNH A 5303	7.7	12.9	7.2	6.0	4.7
Pseudocrypturus cercanaxius					
Sibea specimen(1)	—	~15.2	—	—	—
BMNH A 4490	—	13.1	<7.3	—	—
WN 80280	8.3(r)	13.5(1)	6.7(1)	~6.4(1)	~4.5(1)
Paracathartes howardae					
USNM 361420	13.1	—	—	10.2	9.1
USNM 361421	—	24.2	13.2	10.6	9.5

TABLE 12.   Measurements of lithornithid radii.

Specimen	Length	Caput Diameter Dor.-Ven.	Caput Diameter Ant.-post.
Lithornis vulturinus			
BMNH A 5204	>>79.8	——	5.3
Lithornis promiscuus			
USNM 336535	103.2	5.9	7.0
AMNH 21900	——	5.8	6.8
Lithornis plebius			
USNM 336534	——	4.0/4.0	5.1/5.0
AMNH 21902	~74.7/>74.5	4.2(1)	4.6(1)
Pseudocrypturus cercanaxius			
Siber specimen(1)	74.5	——	——
Paracathartes howardae			
USNM 361422	——	7.2	8.1
USNM 361423	——	6.8	8.5
USNM 361424	110.0	7.3	9.0

TABLE 13.   Measurements of lithornithid radii. Specimens UM 73103 and WN 80280 are only tentatively referred to the taxa listed here.

Specimen	Midshaft Minimum Diameter	Midshaft Maximum Diameter	Distal Width
Lithornis vulturinus			
BMNH A 5204	3.3	3.4	——
BMNH 38934	3.1	3.5	——
Lithornis nasi			
BMNH A 5455	2.9(1)	3.1(1)	8.6/>7.8
UM 73103	——	——	8.6
Lithornis celetius			
USNM 336200	3.4	3.6	9.2
PU 16961	3.3	3.6	——
Lithornis promiscuus			
USNM 336535	3.9	4.3	10.8
AMNH 21900	——	——	>9.5
UM 69343	3.7	4.1	9.7

Lithornis plebius

USNM 336534	2.4(1)	3.0(1)	7.5(r)
AMNH 21902	2.6/2.6	3.2/3.0	>7.4(r)

Pseudocrypturus cercanaxius

Siber specimen	——	——	7.9/7.8
WN 80280	2.7	3.1	7.0

Paracathartes howardae

USNM 361422	4.6	4.9	——
USNM 361424	4.4	5.0	14.2
USNM 361441	——	——	12.4

TABLE 14. Measurements of lithornithid ulnae.

Specimen	Length	Proximal Width; Ventral Flush with Caliper	Proximal Width; Dorsal Flush with Caliper	Midshaft Maximum Diameter
Lithornis nasi				
BMNH 5200	——	9.5	8.2	——
BMNH A 5455	>>80.0	10.9	8.6	5.5
WN 81373	~86.0	——	——	——
Lithornis celetius				
USNM 290554	>>85.5	10.0	9.0	5.4
PU 23484	>>85.5	——	——	5.4
Lithornis promiscuus				
USNM 336535(1)	105.5	12.2	10.8	6.9
Lithornis plebius				
USNM 336534(1)	76.6	8.0	7.4	4.6
Pseudocrypturus cercanaxius				
Siber specimen(1)	79.2	——	——	——
Paracathartes howardae				
USNM 361425	~120.0	15.2	12.7	9.8
USNM 361426	>116.7	——	——	10.5

TABLE 15. Measurements of lithornithid ulnae.

Specimen	Midshaft Minimum Diameter	Distal Condyle Ant.-post.	Distal Condyle Dor.-ven.
Lithornis vulturinus			
BMNH A 5204(1)	——	9.9	8.0
BMNH 38934	4.5	——	——
Lithornis nasi			
BMNH A 5455	4.7	9.3	7.8
Lithornis celetius			
USNM 290554	4.1	——	——
PU 23484	4.6	>9.1	~7.0
Lithornis promiscuus			
USNM 336535	5.3/5.5	11.8/11.7	9.1/9.0
AMNH 21900	6.4	11.3	8.6
UM 69343	5.4	~11.3	8.9
Lithornis plebius			
USNM 336534(1)	3.7	8.0	6.5
Paracathartes howardae			
USNM 361425	6.7	~15.9	10.8
USNM 361426	7.0	15.3	11.3
USNM 361427	6.9	15.4	11.6

TABLE 16. Measurements of lithornithid carpometacarpi. Specimen WN 80280 is only tentatively referred to *Pseudocrypturus cercanaxius*.

Specimen	Length	Proximal Articular Width Dor.-ven.	Proximal Height Ant.-post.	Alular Metacarpal Length Prox.-dist.
Lithornis vulturinus				
BMNH A 5204	——	>5.0	——	——
Lithornis nasi				
BMNH A 5455	——	5.9(1)	12.5(1)	7.2 7.3
WN 79238	43.9	——	11.9	6.8
Lithornis celetius				
USNM 290554	>48.5	5.8	11.4	7.1

Lithornis promiscuus

USNM 336535	58.5(r)	7.7(r)	15.2(r)	8.9/8.5
AMNH 21900	>>59.1/63.1	6.8	14.2	9.1
UM 69343	59.6	6.9	14.9	7.9

Lithornis plebius

USNM 336534	41.3/41.8	5.0/4.7	10.4/10.8	5.8/~6.8
AMNH 21902	——	4.9	10.2	——
UM 83892	——	4.9	——	——

Pseudocrypturus cercanaxius

Siber specimen___	——	——	6.5/6.5	
WN 80280	42.3	——	11.9	7.4

Paracathartes howardae

USNM 361445	>61.2	9.1	18.8	9.4

TABLE 17. Measurements of lithornithid carpometacarpi.

Specimen	Major Metacarpal Ant.-post. Diameter	Major Metacarpal Dor.-ven. Diameter	Distal Width	Distal Height Articular Surface Major Metacarpal
Lithornis celetius				
USNM 290554	3.1	4.4	——	——
Lithornis promiscuus				
USNM 336535	4.2(r)	5.4(r)	9.7/9.7	6.4/6.4
AMNH 21900	4.2(1)	5.3/5.5	~9.4/~8.8	5.8(r)
UM 69343	3.9	5.3	9.0	6.4
Lithornis plebius				
USNM 336534	2.9/2.9	3.6/3.4	6.5/7.1	4.1/4.2
AMNH 21902	2.9	3.7	——	——
Paracathartes howardae				
USNM 361445	5.3	7.1	——	——
USNM 361446	4.8	7.7	——	——

TABLE 18. Measurements of lithornithid innominates. "Height" is measured dorso-ventrally and "length" is measured from the acetabulum.

Specimen	Ant. Ilium Height (Minimum)	Ant. Ilium Length	Post. Ilium Length	Post. Ilium Width	Ischium Length	Ischium Height (Maximum)
Lithornis celetius						
USNM 290601	12.3	>36.0	—	16.5	—	10.8
PU 23485	13.5	39.7	—	—	—	—
Lithornis promiscuus						
USNM 336535	14.7/14.7	—	35.0(r)	16.0(r)	37.0(r)	13.2/12.8
AMNH 21903	—	—	—	16.0	—	10.0
Lithornis plebius						
USNM 336534	8.8/10.5	—	23.5(r)	9.5(r)	33.8(r)	8.7 7.9

TABLE 19.   Measurements of lithornithid femora. Specimen WN 80280 is only tentatively referred to *Pseudocrypturus cercanaxius*.

Specimen	Length	Ant.-post. Diameter Head	Length Head	Ant.-post. Diameter Shaft
Lithornis vulturinus				
BMNH A 5204	—	>5.6	~13.2	—
BMNH A 5278	—	5.9	14.1	—
Lithornis nasi				
BMNH A 5455	—	5.9	13.5	6.3
WN 75124	—	—	13.9	—
?Lithornis hookeri				
BMNH A 5421	—	~4.0	—	3.9
Lithornis celetius				
USNM 290601	—	6.1	13.6	<6.9
PU 16961	>>73.0	—	—	>6.0
Lithornis promiscuus				
USNM 336535	>83.0(1)	6.9(1)	—	7.3(1)
AMNH 21900	—	6.3	14.5	—
UM 69343	82.3(1)	6.0(1)	16.1(1)	7.0(1)
Lithornis plebius				
USNM 336534	64.6/65.1	4.9/5.0	11.7/>11.0	4.9/5.0
UM 83892	—	—	—	4.9
AMNH 21902	—	4.9	11.6	5.0
Pseudocrypturus cercanaxius				
Siber specimen	~63.0/~62.7	—	—	—
WN 80280	—	—	12.5	—
Paracathartes howardae				
USNM 361443	—	9.0	—	—
USNM 361412	109.2	9.3	>20.3	>8.8

TABLE 20. Measurements of lithornithid femora. Specimens UM 73103 and WN 80280 are only tentatively referred to the taxa listed here.

Specimen	Ant.-post. Trochanter (Prox. End)	Distal Width Condyles	Ant.-post. Medial Condyle	Ant.-post. Lateral Condyle (Tibio-fibular crest)	Length Articular Surface Medial Condyle
Lithornis vulturinus					
BMNH A 4270	>9.0	12.5	10.1	12.6	8.2
BMNH A 5204	—	—	—	—	—
BMNH A 5278	—	13.0	9.7	12.1	8.1
Lithornis nasi					
BMNH A 5200	10.0	12.9	—	~11.7	8.2
BMNH A 5455	9.4	—	—	—	—
WN 75124	—	—	—	—	—
WN 79238	—	—	—	11.1	—
UM 73103	9.7	12.9	9.0	—	7.9
?Lithornis hookeri					
BMNH A 5421	6.5	—	—	—	—
Lithornis celetius					
USNM 290601	10.0	—	—	—	—
PU 16961	—	>12.7	8.7	11.2	8.3
Lithornis promiscuus					
USNM 336535	12.2(r)	16.1(1)	11.9(1)	14.4(1)	9.7(1)
AMNH 21900	11.0	14.3	10.3	13.4	8.7
UM 69343	—	15.5	11.5	13.6	9.5

Specimen	Total Length	Distal Width	Ant.-post. Inner Condyle	Ant.-post. Outer Condyle	Length Anterior Cnemial Crest
Lithornis plebius					
USNM 336534	8.2/8.6	10.9/10.9	8.3/8.5	10.0. 10.3	7.2/6.9
AMNH 21902	8.1	—	—	—	—
Pseudocrypturus cercanaxius					
BMNH A 5424	—	>10.9	9.3		7.5
WN 80280	8.5	10.9	—	~10.0	6.9
Paracathartes howardae					
USNM 361412	>13.4	>20.5	>13.8	18.3	12.8

TABLE 21. Measurements of lithornithid tibiotarsi. Specimen WN 80280 is only tentatively referred to *Pseudocrypturus cercanaxius*.

Specimen	Total Length	Distal Width	Ant.-post. Inner Condyle	Ant.-post. Outer Condyle	Length Anterior Cnemial Crest
Lithornis vulturinus					
BMNH A 5198	—	11.4	11.6	10.0	—
BMNH A 5199	—	11.2	10.7	9.7	—
Lithornis nasi					
BMNH A 5200	—	10.3	9.5	8.8	—
BMNH A 5455	—	—	10.2	—	—
WN 74046	—	10.3	—	8.5	—
WN 79238	—	10.1	—	8.8	—
WN 81373	112.5	10.5	9.5	9.1	—
WN 83445	—	11.0	9.7	9.0	—

Continued

TABLE 21 (Continued)

?Lithornis hookeri					
BMNH A 5202	—	8.1	7.6	7.0	—
Lithornis promiscuus					
USNM 336535(r)	129.6	13.4	12.4	11.6	19.5
AMNH 21900	>>112.0	~14.3	~12.7	~11.9	16.3
UM 69343	>130.0	—	—	—	—
Lithornis plebius					
USNM 336534	97.2/95.8	10.0/9.8	9.0 8.7	8.7 8.3	13.3 13.3
AMNH 21902	—	9.0	8.7	8.0	—
Pseudocrypturus cercanaxius					
Siber specimen	90.3/89.0	~10.5(r)	—	—	—
WN 80280	—	8.9	8.0	7.5	13.2
Paracathartes howardae					
ROM 22658	—	>15.3	15.2	14.8	—
USNM 361407	—	17.5	15.7	15.0	—
USNM 361408	177.4	17.5	15.9	15.2	—
USNM 361409	179.0	16.0	15.8	15.3	26.3
USNM 404749	172.8	17.3	15.8	14.9	25.1
UM 76547	—	17.8	16.5	15.0	—

TABLE 22. Measurements of lithornithid tibiotarsi. Specimens WN 80280 and BMNH A 5424 are only tentatively referred to *Pseudocrypturus cercanaxius*.

Specimen	Med.-lat. Width Proximal Condyles	Length Lateral Cnemial Crest	Length Both Cnemial Crests	Med.-lat. Diameter Shaft	Ant.-post. Diameter Shaft
Lithornis vulturinus					
BMNH A 5199	—	—	—	6.9	5.1
Lithornis nasi					
WN 79238	10.0	—	13.9	5.8	—
WN 81373	—	—	—	5.9	4.2
Lithornis celetius					
USNM 290554	—	—	—	6.6	5.4
Lithornis promiscuus					
USNM 336535(r)	13.8	13.3	19.0	7.7	6.0
AMNH 21900	11.6	13.1	16.0	—	—
UM 69343	—	—	—	7.3	6.3
Lithornis plebius					
USNM 336534	9.2/9.0	10.1/9.8	13.0/13.0	5.1/5.0	4.1/3.9
Pseudocrypturus cercanaxius					
Siber specimen					
WN 80280	9.0	—	—	7.9 ~7.1	—
BMNH A 5424	9.2	9.5	13.0	4.8	3.9
Paracathartes howardae					
USNM 361408	17.8	>18.3	24.7	9.9	7.4
USNM 361409	16.9	19.3	25.4	9.4	6.7
USNM 404749	17.6	19.5	24.8	9.6	7.4

TABLE 23.   Measurements of lithornithid fibulae.

Specimen	Ant.-post. Femoral Articulation	Length of Femoral Articulation to Insertion Biceps Loop
Lithornis nasi		
BMNH A 5455	8.0	——
Lithornis celetius		
USNM 336200	8.4	26.2
Lithornis promiscuus		
USNM 336535	9.7	28.8
AMNH 21900	9.8/9.9	——
Lithornis plebius		
USNM 336534	7.0	——
Paracathartes howardae		
USNM 361413	13.1	38.0
USNM 361414	12.5	38.3
USNM 361442	13.0	——
USNM 361444	13.2	——

TABLE 24. Measurements of lithornithid tarsometatarsi. Specimens UM 73103, PU 23482, and WN 80280 are only tentatively referred to the taxa listed here.

Specimen	Length	Proximal Width	Proximal Depth	Distal Width	Width Middle Trochlea	Ant.-post. Dia. Shaft
Lithornis vulturinus						
BMNH A 225	>>63.5	10.9	10.2	—	—	—
BMNH A 3681	—	11.1	9.9	—	—	—
BMNH A 5195	—	11.7	—	—	—	—
BMNH A 5197	—	11.5	10.5	—	—	—
Lithornis nasi						
BMNH A 5455	65.2	10.0	8.7	11.7	5.1	—
WN 79238	—	—	—	11.6	—	—
WN 75071	—	—	—	—	4.1	—
WN 82403	—	9.1	7.8	—	—	—
PU 23482	—	11.2	10.0	—	—	—
UM 73103	—	10.9/10.8	9.8(r)	12.6(1)	5.0(1)	4.1(1)
?Lithornis hookeri						
BMNH A 3701	—	>6.8	6.8	—	—	—
BMNH A 4278	—	7.9	—	—	—	—
Lithornis celetius						
USMN 290554	—	—	—	13.7	5.9	4.6
PU 23484	—	—	—	12.8	5.3	5.8
PU 16961	—	11.6	10.6	—	—	—
PU 20510	—	10.3	—	—	—	—
Lithornis promiscuus						
USNM 336535	~76.0	~13.8	11.6	14.3	—	5.0
AMNH 21900	—	12.3	10.6	14.1	5.7	4.6
UM 69343	—	—	—	—	5.7/5.2	4.8

Continued

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TABLE 24 (Continued)

Specimen	Med.-lat. Width Shaft	Length Inner Minus Middle Trochlea	Length Outer Minus Middle Trochlea	Ant.-post. Width Inner Trochlea	Ant.-post. Width Middle Trochlea	Ant.-post. Width Outer Trochlea
Lithornis plebius						
USNM 336534	59.7	9.8	8.2	10.9	5.0	4.7
Pseudocrypturus cercanaxius						
Siber specimen	48.1/47.1	5.9(r)	—	10.9(1)	4.3(1)	—
WN 80280	—	9.1	7.7	9.9	4.1	—
Paracathartes howardae						
USNM 361402	113.5	16.8	—	21.1	8.1	6.5
USNM 361403	110.5	—	—	—	—	6.8
USNM 361404	—	16.8	15.0	19.9	7.9	6.3
USNM 361405	112.8	16.4	15.0	20.0	8.2	5.9
USNM 361406	115.0	17.2	15.6	19.2	7.5	6.8
USNM 404747	109.8	~17.8	—	19.7	8.2	6.0
USNM 404748	—	—	—	—	—	5.6

TABLE 25. Measurements of lithornithid tarsometatarsi. Specimens UM 73103 and WN 80280 are only tentatively referred to the taxa listed here.

Specimen	Med.-lat. Width Shaft	Length Inner Minus Middle Trochlea	Length Outer Minus Middle Trochlea	Ant.-post. Width Inner Trochlea	Ant.-post. Width Middle Trochlea	Ant.-post. Width Outer Trochlea
Lithornis vulturinus						
BMNH A 225	5.8	—	—	—	—	—
BMNH A 3681	5.2	—	—	—	—	—

Lithornis nasi						
BMNH A 5455	—	4.1	2.6	6.3	6.0	7.1
WN 79238	5.2	3.3	~2.9	—	—	—
UM 73103	5.3(1)	4.0	2.9	>6.1	6.2	7.3
Lithornis celetus						
USNM 290554	—	4.6	2.8	>6.5	6.4	8.0
PU 23484	—	5.8	3.6	6.1	5.9	7.3
Lithornis promiscuus						
USNM 336535	6.8	—	—	—	—	—
AMNH 21900	6.0	4.3	3.5	7.4	6.6	8.0
UM 69343	—	3.4	3.4	—	6.8	—
Lithornis plebius						
USNM 336534	—	3.2	2.2	5.6	—	5.6
Pseudocrypturus cercanaxus						
WN 80280	—	3.3	2.5	5.7	4.7	5.1
Paracathartes howardae						
USNM 361402	7.8	6.4	5.4	10.2	9.4	11.1
USNM 361403	7.7	—	—	—	—	11.5
USNM 361404	8.0	—	—	9.4	—	—
USNM 361405	7.9	5.0	4.9	10.0	9.5	>10.9
USNM 361406	8.6	6.5	4.8	9.9	9.8	11.0
USNM 404747	7.3	4.7	4.5	10.1	9.3	10.7
USNM 404748	7.9	5.9	4.6	9.4	9.1	10.7

TABLE 26.   Measurements of lithornithid phalanges.

Specimen	Identification	Length
Lithornis celetius		
USNM 336200	Prox. phal. dig. II	21.4
USNM 336200	Dist. phal. dig. III	17.4
PU 16961	Dist. phal. dig. III	17.5
USNM 336200	Mid. phal. dig. IV	8.8
USNM 336200	Dist. phal. dig. IV	11.8
USNM 336200	Term. phal. ? dig.	9.0
Lithornis promiscuus		
USNM 336535	Prox. phal. dig. I	16.5
USNM 336535	Prox. phal. dig. III	20.8/21.2
USNM 336535	Mid. phal. dig. III	17.3
USNM 336535	Dist. phal. dig. III	20.9
USNM 336535	Prox. phal. dig. IV	14.3
USNM 336535	Dist. phal. dig. IV	13.4
USNM 336535	Term. phal. ? dig.	14.3
USNM 336535	Term. phal. ? dig.	>11.9
USNM 336535	Term. phal. ? dig.	>11.2
USNM 336535	Term. phal. ? dig.	10.1
USNM 336535	Term. phal. ? dig.	10.0
USNM 336535	Term. phal. ? dig.	9.2
Pseudocrypturus cercanaxius		
Siber specimen (1)	Articulated dig. I	19.1
Siber specimen (1)	Prox. phal. dig. I	12.4
Siber specimen (1)	Term. phal. dig. I	8.0
Siber specimen (1)	Articulated dig. II	36.2
Siber specimen (1)	Prox. phal. dig. II	15.2
Siber specimen (1)	Mid. phal. dig. II	14.0
Siber specimen (1)	Term. phal. dig. II	10.0
Siber specimen (1)	Articulated dig. III	49.0
Siber specimen (1)	Prox. phal. dig. III	14.1
Siber specimen (1)	Mid. phal. dig. III	13.8
Siber specimen (1)	Dist. phal. dig. III	14.9
Siber specimen (1)	Term. phal. dig. III	10.9
Siber specimen (1)	Articulated dig. IV	38.9
Siber specimen (1)	Prox. phal. dig. IV	~10.0
Siber specimen (1)	Prox. mid. phal. dig. IV	~ 7.7
Siber specimen (1)	Dist. mid. phal. dig. IV	~ 7.0
Siber specimen (1)	Dist. phal. dig. IV	~ 9.2
Siber specimen (1)	Term. phal. dig. IV	8.9
Paracathartes howardae		
USNM 404770	Prox. phal. dig. I	20.8
USNM 404771	Prox. phal. dig. I	18.6
USNM 404759	Prox. phal. dig. II	26.4
USNM 404760	Prox. phal. dig. II	26.2

USNM 404761	Prox. phal. dig. III	27.1
USNM 404762	Prox. phal. dig. III	27.1
USNM 404763	Prox. phal. dig. III	26.3
USNM 404764	Prox. phal. dig. III	26.4
USNM 404765	Prox. phal. dig. III	27.8
USNM 404766	Prox. phal. dig. III	27.8
USNM 404772	Mid. phal. dig. III	21.5
USNM 404773	Mid. phal. dig. III	21.4
USNM 404774	Mid. phal. dig. III	21.7
USNM 404775	Mid. phal. dig. III	22.2
USNM 404776	Dist. phal. dig. III	22.4
USNM 404777	Dist. phal. dig. III	22.6
USNM 404778	Dist. phal. dig. III	21.1
USNM 404779	Dist. phal. dig. III	22.0
USNM 404781	Dist. phal. dig. III	22.4
USNM 404767	Prox. phal. dig. IV	18.7
USNM 404768	Prox. phal. dig. IV	17.9
USNM 404769	Prox. phal. dig. IV	19.4
USNM 404782	?Mid. phal. dig. IV	12.9
USNM 404783	?Mid. phal. dig. IV	12.6
USNM 404784	?Mid. phal. dig. IV	12.5
USNM 404785	?Mid. phal. dig. IV	12.2
USNM 404786	Dist. phal. dig. IV	15.6
USNM 404787	Dist. phal. dig. IV	15.9
USNM 404789	Terminal phal. (? dig.)	19.3
USNM 404790	Terminal phal. (? dig.)	15.8
USNM 404791	Terminal phal. (? dig.)	15.5
USNM 404792	Terminal phal. (? dig.)	>14.0
USNM 404793	Terminal phal. (? dig.)	15.0
USNM 404794	Terminal phal. (? dig.)	>13.3
USNM 404795	Terminal phal. (? dig.)	13.7
USNM 404796	Terminal phal. (? dig.)	>12.9
USNM 404797	Terminal phal. (? dig.)	>11.5
USNM 404798	Terminal phal. (? dig.)	12.4
USNM 404799	Terminal phal. (? dig.)	14.1
USNM 404800	Terminal phal. (? dig.)	13.9

TABLE 27.   List of characters used in Figures 39 and 40; p = primitive character state, d = derived character state, d1, d2, d3, d4 = derived characters in a transformational sequence; di and dii = bidirectional derived characters; arrow = reversal to a more primitive character state; triangle = convergent character state. Combinations of letters, e.g., pdl, indicate that both states are found within that taxon. See text for discussion of some characters.

1. Pattern of bone microvascularization in tibiotarsus: p. predominantly oriented in the transverse plane forming a pattern of concentric circles; di. randomly branching and anastomosing; dii. longitudinal, arranged parallel to the long axis of the bone.
2. Feathers: p. absent; d. present.
3. Teeth: p. present; d. absent.
4. Splenial: p. extending rostrally to or near to the mandibular symphysis and unfused with other mandibular elements; d. small and fused with other mandibular elements.
5. Vomer and premaxillae: p. articulated or fused; d. not articulated.
6. Palatal complex of bones: p. fused or ankylosed; d. intrapterygoid joint present.
7. Basipterygoid processes: p. present; d. absent.
8. Quadrate: p. reptilian; d1. avian without condylar pterygoid articulation; d2. avian with condylar pterygoid articulation.
9. Coronal suture: p. unfused in adult; d. fused in adult.
10. Occipital condyle: p. large; d. small.
11. Foramen jugulare spurium: p. not applicable; d1. present; d2. absent.
12. Rhamphothecal grooves: p. absent; d1. represented only by a series of foramina that resemble the rhamphothecal grooves; d2. present.
13. Zygomatic process: p. long but questionably homologous or not applicable; di. long; dii. short.
14. Internarial septum: p. absent; d. present.
15. Quadrate-retroarticular process articulation: p. absent; d. present.
16. Palatal spines: p. absent; d. present.
17. Tympanic cavity: p. absent or not applicable; d1. large but lacking a caudal wall; d2. small; d3. large forming most caudal portion of cranium.
18. Postorbital process: p. small; d. large and rounded.
19. Prefrontals: p. short; d. long.
20. Olfaction: p. poor; d. macrosmatic.
21. Sternum: p. absent; d1. carinate; d2. ratite.
22. Costal processes of sternum: p. not applicable; d1. few; d2. many.
23. Notches in caudal border of sternum: p. not applicable; d1. absent; d2. deep notches present.
24. Coracoidal sulci of sternum: p. not applicable; d1. crossed; d2. uncrossed.
25. Scapula and coracoid: p. not fused; d. fused together to form scapulocoracoid.
26. Articulation of scapula and coracoid: p. simple; d1. reversed as in Enantiornithes; d2. avian.
27. Coracoid: p. flat and wide; d. cylindrical or narrow.
28. Shaft of coracoid: p. not applicable; d1. relatively stout; d2. long and very narrow.
29. Furcula: p. clavicles not fused; d1. clavicles fused, no hypocleideum; d2. clavicles fused and a hypocleideum present.
30. Acromion of scapula: p. absent; d1. large; d2. styliform; d3. reduced; d4. not applicable.

31. Bicipital crest of humerus: p. poorly developed; d1. knob-like; d2. expanded.
32. Pectoral crest of humerus: p. pronounced and arcuate; d. reduced and proximally localized.
33. Configuration of humerus: p. short and curved; d1. long and curved; d2i. short and straight; d2ii. vestigial or useless for flight; d3. non-pneumatic, long, and spindly, useless for flight; d4. as in (d3) but longer.
34. Internal tuberosity of humerus: p. poorly developed; d1. narrow; d2. round; d3. proximally procumbent.
35. Caput of humerus: p. small and narrow; d. large and spherical.
36. Tricipital grooves of humerus: p. absent or poorly developed; d. well developed.
37. Antebrachium: p. short and muscular; d. elongate and tendinous.
38. Carpometacarpus: p. carpals and metacarpals unfused in adult; d1. carpals and metacarpals fused in adult; d3. carpometacarpus vestigial; d3. accessory foramina present between each of the metacarpals; d4. as in (d3) but better developed and more consistently ossified.
39. Notarium: p. absent; d. present.
40. Articulation of synsacrum and innominates: p. unfused; d. fused.
41. Caudal vertebrae: p. lizard-like; d1. free caudal vertebrae with short transverse processes and pygostyle rudimentary; d2. free caudal vertebrae with long transverse processes and pygostyle well developed.
42. Pelvis: p. wide; d. narrow.
43. Acetabulum: p. at least half of acetabulum positioned ventral to ventral border of ilium; d. positioned more dorsally.
44. Ilioischiadic foramen: p. ilium and ischium not fused caudally to circumscribe ilioischiadic foramen; d1i. ilium and ischium fused caudally but foramen large and elongate; d1ii. foramen small.
45. Caudal ischium: p. rounded, truncate, or terminates abruptly; d. tapered.
46. Insertion of iliotrochanteris caudalis muscle on femur: p. not applicable; d1. centrally located near axis of rotation of femur; d2. located on elevated trochanteric crest.
47. Configuration of femur: p. long and curved; d. short and straight.
48. Osseous tendinal bridge of tibiotarsus: p. absent; d. present.
49. Tarsometatarsus: p. metatarsals not fused or incompletely fused in adult; d1. metatarsals completely fused, hypotarsus simple; d2. hypotarsus complex with canals.
50. Interosseous foramen of tarsometatarsus: p. not applicable; d1. large; d2. small.
51. Number of toes: p. four; d1. three; d2. two.
52. Middle trochlea of tarsometatarsus: p. symmetrical in anterior view; d. asymmetrical in anterior view.
53. Proximal tarsometatarsus: p. lacking "winged" processes of the medial and lateral cotylae; d. "winged."
54. Overall size: p. not applicable to avian clade; d1. small; d2. large.
55. Parental care: p. by males (following Elżanowski, 1985); d. by females.
56. Pterygoid fossa: p. absent; d. present.

FUNCTIONAL ANATOMY AND ECOLOGY OF THE LITHORNITHIFORMES

I cannot overemphasize the similarity of the Lithornithiformes and the Tinamiformes, although I consider their similarity to be symplesiomorphous (see Phylogenetic Analysis, p. 121). The analysis of the functional anatomy and paleoecology of the Lithornithiformes is most appropriately made as a comparison with the Tinamiformes, the group to which they are phenetically most similar and from which they presumably diverged.

This discussion is divided into four parts: (1) the head and feeding apparatus; (2) the flight apparatus; (3) the pelvic appendage; and (4) breeding ecology. A preliminary note about the paleoenvironment of Lithornithiformes is fundamental to these discussions.

Gingerich (1976b) writes, "The flora of western North America in the Paleocene was largely a temperate flora, including many of the trees still common today, such as elm, oak, hickory, and conifers. A smaller warm temperate element including palms and breadfruit was also present." Leaves of elm-like trees and either terrestrial or fresh water gastropods are abundantly preserved in the vicinity of the Tiffanian Bangtail Quarry, the type locality of *Lithornis celetius*. Gingerich continues, "The early Eocene of North America witnessed a general warming from the late Paleocene [i.e., Tiffanian] temperate climate to a warmer subtropical one." Rose (1981) adds, "One may envision the northern Bighorn Basin during the Clarkforkian as a warm, humid, forested floodplain at low elevation. Numerous meandering streams crossed the landscape, and channel relocation left many oxbow lakes of standing water, although conditions were probably drier than in the Tiffanian. Fossil floras of the Clarkforkian indicate a warm temperate to subtropical climate, and the sediments reflect soil formation in a climate with alternating wet and dry conditions. The vertebrate fauna was relatively rich, and included terrestrial and aquatic forms. The Clarkforkian ecosystem may have resembled those of warm temperate or subtropical wooded floodplains, such as exist in southeast Asia today."

There are several lines of evidence that suggest lithornithids preferred to live near bodies of water. Tiffanian lithornithid fossils from Bangtail have been found in silty lenses that probably represent overbank deposits or point bar sequences (pers. obs.) Calcareous nodules from both the Tiffanian and Clarkforkian of North America often contain remains of macerated plants (possibly palm wood, L. J. Hickey, pers. comm.). Calcareous nodules contain lithornithid bones turned up at angles to one another more often than lying horizontally in articulation. Burrows up to 3 cm in diameter are common in these nodules. I interpret such nodules as representing a bioturbated, possibly submerged, muddy substrate. The presence of eggshells in these nodules further demonstrates that lithornithids were making more than just casual visits to the places in which they were fossilized. Two

specimens of *Pseudocrypturus* were found in the marlstones of the Green River Formation, which is recognized as representing a lake deposit. Last, specimens collected from the London Clay are preserved along with a mixture of marine (e.g., shark) and terrestrial (e.g., small mammals) vertebrates. These are believed to have been deposited at a depth of about 30 m. Clearly, lithornithids and other terrestrial vertebrates must have been carried to the North Sea Basin, where they were deposited by rivers, along which they presumably lived. Birds that simply died on the seashore would probably not be deposited at such depths.

HEAD AND FEEDING APPARATUS

In general, the neurocranium of lithornithids is similar in almost every detail to that of tinamous, e.g., *Tinamus* and *Eudromia*, although the zygomatic process is longer, as in *Rhynchotus*. *Paracathartes* (Fig. 5) may be an exception in that its bony processes and fossae may be larger and more like those of ratites, e.g., *Casuarius*. However, these differences are paralleled by small and large species of the genus *Larus* (Laridae) and are possibly allometrically correlated. There is not as much size variation in any single genus of Tinamidae as there is in the genus *Larus,* so the existence of cranial allometry in tinamous is difficult to prove. Nevertheless, tinamous do seem to exhibit cranial allometry. Small species, such as *Nothoprocta pentlandii,* exhibit very round skulls with small processes and shallow fossae, whereas the brains of larger species, such as *N. taczanowskii,* are not significantly larger than those of their smaller congeners but the skulls are larger, more robust, and have larger processes and deeper fossae.

There are three notable differences between the skulls of tinamous and those of lithornithids. Lithornithids (1) lack the submeatic prominence of the quadrate (Elżanowski, 1987) that is characteristic of tinamous, (2) have greater osseous compartmentalization of the nasal cavity, and (3) have a more kiwi-like jaw apparatus.

Both the osseous compartmentalization of the nasal cavity and specializations of the jaw apparatus reflect a more kiwi-like than tinamou-like foraging behavior of lithornithids. Both tinamous and kiwis are said to forage in ground litter for invertebrates, berries, and seeds (Van Tyne and Berger, 1971). However, Beecher (1962) and Bock (1963) speculate, with good reason, that kiwis probe their bill and are capable of extreme rostral rhynchokinesis, as is the case in many scolopacids.

The base of the bill in lithornithids is reinforced by the extensive internarial septum, osseous parasagittal septa, ventral curvature of the lateral edge of the dorsal nasal bar, and the shallow fossa of the dorsal surface of the bill in the region of the fronto-nasal junction, as in kiwis. Reinforcement of the base of the bill restricts cranial kinesis to more rostral portions of the bill ("distal rhynchokinesis" of Zusi, 1984; see Fig. 36), which is not reinforced by three dimensional osseous structures. Convergently similar reinforcement of the base of the bill is also present in snipes (Scolopacidae), which can raise

the extreme rostral tip of their upper bill without depressing the mandible. This enables them to catch prey underground without opening their entire bill against the resistant earth (Marinelli, 1928; Beecher, 1962; Bock, 1963). The bill of lithornithids is delicate, intermediate in length between those of tinamous and kiwis, and has foveae for nervous corpuscles (for the rostral rami of the mandibular nerve; Fig. 7) that are larger and more conspicuous than those in tinamous or even kiwis. They were, therefore, probably sensitive-billed probers. In contrast, kiwis seem to be more dependent on olfactory cues than on tactile recognition of prey.

The unique structure of the retroarticular process and the quadrato-mandibular articulation of kiwis and lithornithids (Fig. 8) is probably a further adaptation to distal rhynchokinesis. In these birds the quadrate fits into a notch in the mandible, buttressed posteriorly by the retroarticular process. This is unlike the condition observed in most birds, in which the quadrate is buttressed only anteriorly by the contracondylus of the mandible (with the exceptions of some Pelecaniformes and Ciconiiformes which, however, restrict antero-posterior movement in a different fashion), such that there may be considerable antero-posterior freedom in the joint.

In most birds, rostral rotation of the quadrate is primarily accomplished by the protractor pterygoidi et quadrati muscle. However, the depressor mandibulae muscle has also been implicated in the protraction of the quadrate in the distally rhynchokinetic snipes (Marinelli, 1928; Beecher, 1962) and protraction has been evoked by direct electrical stimulation of the depressor in other birds (Zusi, 1967). The lithornithid-kiwi jaw articulation may relate to the facilitation of rostral rotation of the quadrate by the depressor mandibulae muscle. If the depressor mandibulae really does pro-tract the mandible in kiwis, then force from the retroarticular process onto the quadrate would necessarily play a role in protraction of the quadrate. The retroarticular processes of lithornithids and kiwis are, in fact, enlarged to bear hypertrophied depressor mandibulae muscles. However, the use of the depressor mandibulae in this action has not been demonstrated electro-myographically in kiwis. Moreover, in scolopacids the retroarticular process does not buttress the quadrate posteriorly, thus the necessity for the lithornithid-kiwi jaw articulation for distal rhynchokinesis is questionable.

FLIGHT APPARATUS

The wing bones of lithornithids employ mechanical advantages that would have enhanced their powers of sustained flight as compared with tinamous (Fig. 37), which are anatomically and biochemically specialized for galliform-like short bursts of flight as an escape mechanism (Stegmann, 1978).

In tinamous and the more specialized families of Galliformes the sternum is greatly lengthened caudally and is deeply incised by notches in the posterior margin that are covered by tough membrane. The elongated sternum maximizes surface area for the origins of the flight muscles, which
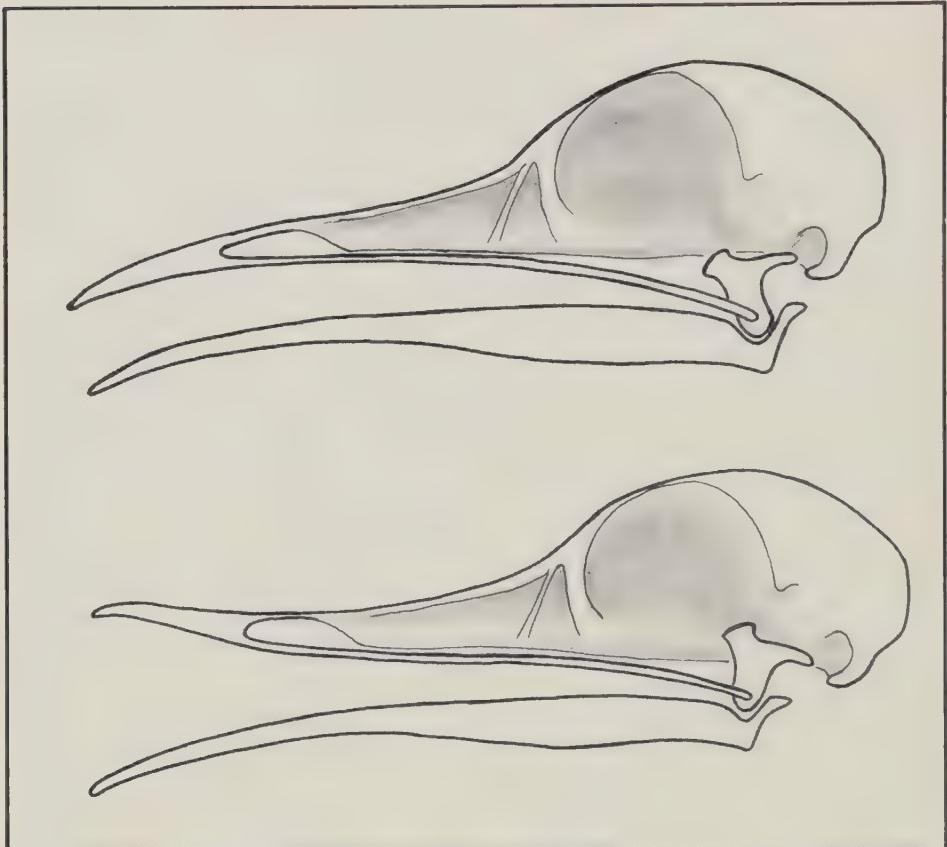
Fig. 36. Distal rhynchokinesis in the skull of lithornithids. Upper: bill at rest; lower: quadrate protracted, premaxillae raised. Note continuity of nasal and interorbital septa, and extreme rostral region of flexion of the dorsal nasal bar.
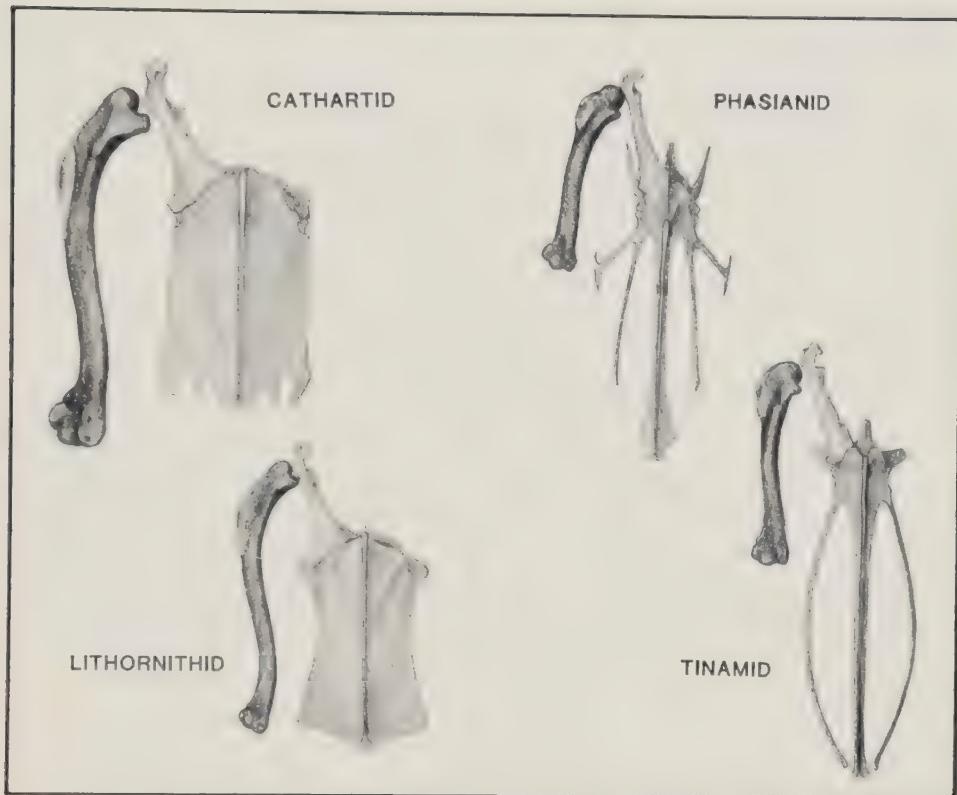
Fig. 37.   Sterna, coracoids, and humeri of two neognathous birds, a New World vulture (Cathartidae: *Cathartes*) and a pheasant (Phasianidae: *Phasianus*), and two paleognathous birds, a lithornithid (*Lithornis*) and a tinamou (*Tinamus*). Note the similarity of the vulture to the lithornithid and of the pheasant to the tinamou, and the difference between these pairs, reflecting the similarities and differences in the behavioral ecologies of these birds.

are massive and powerful. The coracoids are mediolaterally narrow, but robust and nearly cylindrical to resist compression and buckling at the sterno-coracoid articulation.

Quite in contrast, the sternum in lithornithids is short, with a truncate, unnotched posterior margin. The coracoids are thin with laterally flared angles and the sterno-coracoid articulation is thin and weak. The breast musculature of lithornithids was comparatively weak and evidently better adapted for sustaining wing posture than for rapid, powerful contractions. The overall configuration is intermediate between the conditions seen in ibises and New World vultures.

There are no modern analogs to the long styliform acromion of the lithornithid scapula. The coracoid and scapula of one undeformed specimen, *Lithornis plebius*, BMNH A 5303, were found in articulation but it is still not clear how the furcula articulated with them. In this specimen, the acromion of the scapula forms the medial wall of the triosseal canal, which is usually formed by a ligament and/or a portion of the furcula in other birds.

The wing of *Lithornis* is relatively longer than it is in tinamous, whereas the wings of *Pseudocrypturus* and *Paracathartes* are relatively shorter and more tinamou-like. The greatest differences in the wing elements between lithornithids and tinamous are in the humerus.

In the humerus of tinamous the caput is large and spherical, the shaft is short and straight, and the insertion of the pectoralis muscle is located far proximally. The shortness of the tinamou humerus speeds movement of the wing because: (1) the musculature is localized proximally and, therefore, there is less distal inertia; (2) the resistance of the air has a shorter lever arm (assuming humerus length is correlated with wing length) with which to resist the force of the flight muscles; and (3) the length of the muscle bellies is limited and, if fiber length is correlatively shorter, the length (and hence duration) of muscle contraction is reduced.

In contrast, the humerus of lithornithids, particularly *Lithornis*, has a narrow caput, a long, curved shaft, and the insertion of the pectoralis muscle is more distally situated on a large, prominent pectoral crest. This morphology is intermediate between those observed in ibises and New World vultures, whose flight is characterized by slow wingstrokes and intermittent gliding. The distally placed insertion of the pectoral muscle achieves greater leverage at the expense of speed. The narrow caput is best suited for slow movement or sustaining an open wing posture. Lengthening of the humerus increases the moment arm of the wing and slows its action by increasing its distal inertia and increasing the lever arm with which air can resist the wing. The curvature of the humerus increases the angle formed by the distal end of the humerus and antebrachium and may be important in sustaining the open wing posture.

Other differences in the humeri of tinamous and lithornithids are the location (ventral versus dorsal) of the insertion of the latissimus dorsi muscle, the configuration (narrow versus round) of the internal tuberosity (insertion of the subcoracoideus and coracobrachialis posterior muscles),

and the insertion of the deltoid muscle (on shaft versus on pectoral crest). The last of these is probably related only to the enlarged insertion of the pectoralis muscle, to which the deltoid muscle is an antagonist. In the condition of these insertions, tinamous parallel phasianids whereas lithornithids parallel ibises and vultures. However, the precise mechanical significance of these characters is not obvious.

The antebrachium of lithornithids was apparently fleshy throughout its length, judging from intermuscular ridges on the radius and ulna. Thus, the distal inertia of the wing was fairly large as compared with most long-winged birds.

The tail of lithornithids was small and weak, much like that of tinamous. The pygostyle of lithornithids is small and poorly fused, although it is relatively larger in smaller species. The free caudal verebrae virtually lack transverse processes. As the development of transverse processes is generally directly correlated with tail size, the retrices of lithornithids were probably very short. By analogy, some megapodes (Galliformes) have long tails and rudimentary pygostyles, but their free caudal vertebrae have well-developed transverse processes. Since the iliocaudal fossa and terminal iliac process of the pelvis, where some of the tail musculature originates, are slightly better developed in lithornithids than they are in tinamous, the lithornithid tail might have been slightly more muscular than that of tinamous. Any such difference was certainly slight.

Hypothetically, paleognathous birds could represent a grade of avian evolution that precedes the invention of a well-developed pygostyle and fanlike tail. Long-winged lithornithids with stubby tails would probably appear bizarre by the standards of modern birds. But, if paleognathous birds diverged from the rest of the class Aves before the evolution or perfection of the pygostyle, then lithornithids may just have had to make the best of the poor equipment with which they were endowed.

PELVIC APPENDAGE

The skeleton of the pelvic appendage in most lithornithids does not differ significantly from that of tinamous in the relative lengths of the elements. The major differences seem to reflect two alternate means of placing the foot under the bird's center of gravity. The knees of tinamous are displaced laterally by the bird's wide body, whereas in lithornithids the legs are closer and are more nearly parallel to one another. Despite this, lithornithids lack important cursorial adaptations of the femur that are present in the femora of tinamous (Fig. 38) and were, therefore, probably no better adapted for cursorial life than are tinamous (see below).

The lithornithid pelvis is best characterized by its similarity to that of tinamous, particularly *Rhynchotus* (Fig. 22). The dorsal surface of the postacetabular ilium in the Lithornithidae is at least as broad as it is in *Rhynchotus*, but is narrower than the pelves of forest-dwelling tinamous. However, the region dorsal to the acetabulum is broader in lithornithids and

bears a well-defined crest, as in the pelvis of the trumpeter, *Psophia*. The most striking feature of the pelvis of lithornithids is the large cavernous ilioischiadic fossa (for want of a better name) formed by the postacetabular elements. This trait is also well-developed, albeit to a lesser extent, in the tinamous of open country, such as *Rhynchotus*. Despite the similarity of the pelves of lithornithids and tinamous of open country, lithornithids probably spent most of their time in and among the trees (see discussion of the claws below). With its well-defined terminal iliac process, the lithornithid pelvis takes on a resemblance to those of hoatzins, cuckoos, and touracos (Opisthocomidae, Cuculidae, and Musophagidae, respectively), members of the "basal land bird assemblage" of Olson (1985).

The ilioischiadic fossa is formed by the ischium, ilioischiadic membrane, and postacetabular ilium. The extent to which the postacetabular ilium contributes to the fossa is limited by the position (medial vs. lateral) of the crest for the attachment of the ilioischiadic membrane on its ventral surface. The iliac contribution to this fossa is much greater in lithornithids than it is in any of the tinamous, so that the surface area for the origins of the extensors of the thigh and long flexors of the leg is larger and the muscle masses lie closer to the midsagittal plane of the body in lithornithids than in tinamous. Both of these attributes would seem to be cursorially adaptive. Not only is the body supported by legs closer to its center of gravity, the muscle mass is concentrated near the center of gravity. Thus, gravity has a shorter lever arm with which to pull the body to one side when the bird is supported by only the contralateral leg. Regardless, in ratites the relative proportions of the appendicular elements are better correlated with cursoriality than is pelvic width. Tinamous and lithornithids have much the same relative proportions of leg elements. Since the large ilioischiadic fossa is well-developed in cuckoos, hoatzins, and touracos, which include both good and poor runners, the functional importance of this morphology is unclear and it may be another primitive avian condition characteristic of lithornithids.

The few well-preserved pelves of lithornithids apparently differ somewhat from species to species in the closure of the ilioischiadic foramen and in the development of the terminal angle of the ischium. The absence of both the distal fusion of the ischium and ilium and the osseous terminal angle of the ischium are either primitive or neotenic characters. There even appears to be intraspecific variation in the dorsoventral height of the preacetabular ilium.

The area for muscle origin is the same regardless of whether the ilioischiadic fossa is membranous or ossified. Thus, the functional difference between *Lithornis celetius*, in which the foramen is apparently closed, and other lithornithids in which it is definitely open, is probably not significant to locomotion. Perhaps it is significant to the laying of large eggs, instead, as the ischium would be more readily deformed if it is not fused to the ilium distally. A survey of tinamou pelves reveals that any such deformation that does take place is not sufficient to result in fracture of the ischium with enough frequency to be documented in museum collections.

Small species of lithornithids exhibit a long and well-developed terminal

angle of the ischium, like that of adult neognathous birds. The caudal ischia of *L. promiscuus* (Fig. 21) and *L. celetius* are rounded and the terminal angles are only slightly better developed than they are in *Eudromia elegans*. Probably all other tinamous lack the terminal angle of the ischium altogether. In tinamous there is a membrane that extends from the truncate posterior margin of the ischium to the terminus of the pubis that probably has approximately the same functional properties as the osseous terminal angle (pers. obs.). Thus, variability of this character is probably functionally insignificant in lithornithids.

Variation in the dorsoventral height of the preacetabular ilium in *Lithornis celetius* probably has more profound functional implications than the variation in the ossification of membranes, described above. It implies a large difference in the area of preacetabular muscle origins in the different morphs, whereas the variation in ossification does not necessarily imply any difference in the areas of origin of postacetabular muscles. This variation appears to be instraspecific and is apparently related to the overall size of an individual bird.

The femur of lithornithids, like those in tinamous and kiwis, is relatively long and curved. Nevertheless, the femora of kiwis and lithornithids differ from those of tinamous in: (1) the lack of a well-developed trochanteric crest; (2) the angle of the antitrochanteric articulation; (3) the poorer femoral articulation, with respect to the less spherical femoral head and less well defined antitrochanteric articulation that does not form as complete a circle around the femoral head; and (4) the (dorsoventrally) smaller medial condyle (see Fig. 38).

The differences in the tinamou and lithornithid trochanteric crests probably relate to the contribution of the iliotrochanteris caudalis muscle in femoral extension. The contribution of this muscle is maximized in many cursorial birds by lengthening the trochanteric crest on which the muscle inserts. The iliotrochanteris caudalis imparts a much more rapid action to the femur than the postacetabular muscles, which insert much more distally and require more extensive contraction to effect femoral movement. However, in birds with a short trochanteric crest, like lithornithids, the iliotrochanteris caudalis may play no significant role in femoral extension, as compared with the postacetabular muscles, because of its relative mechanical disadvantage.

In tinamous the articulation for the antitrochanter indicates that the femur is directed relatively laterally. The articulation, further, seems to impart rotation of the femur around the longitudinal axis of the shaft during flexion and extension of the thigh. This rotation results from the angle of this articulation to the shaft (although this is actually somewhat variable in different individuals of tinamous). On the other hand, the axis of rotation of the femur of lithornithids is more nearly perpendicular to the shaft. Thus, flexion and extension of the lithornithid femur is closer to the sagittal plane.

The relative size of the medial condyle of the femur is also related to the extent to which the plane of flexion and extension of the thigh approaches
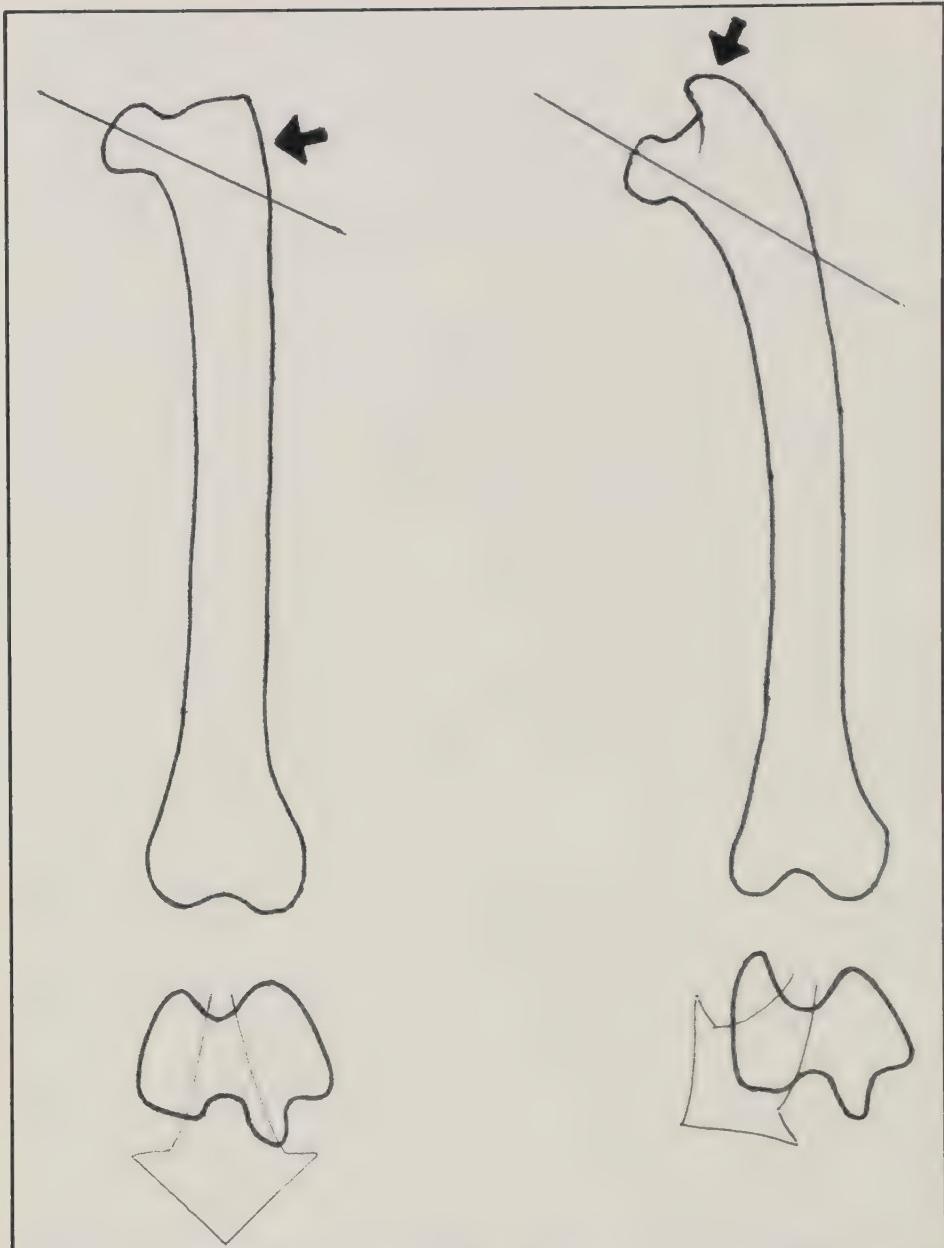
Fig. 38. Femora of lithornithid (left) and a tinamou (right), showing differences in functional anatomy. Upper figures: outline of anterior aspect, straight line through femoral head shows axis of rotation of femur, solid arrow shows insertion of the iliotrochanteris caudalis muscle; the lever arm for this muscle is longer in the tinamou. The carrying angle of the femur is greater in the tinamou, such that the knee is directed more laterally than in the lithornithid. Lower figures: outline of distal aspect; in the tinamou there is a greater medial vector of the patellar ligament (arrow), because of the larger carrying angle, thus the medial condyle is more pronounced to oppose the patellar ligament.

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the sagittal plane. The larger medial condyle of tinamous is the combined result of its angle of articulation with the tibiotarsus and better developed medial patellar ridge. A more laterally directed knee, like that in tinamous, imparts a greater medial vector to the patellar ligament under tension than the knee joint of tinamous and kiwis, which lies closer to the sagittal plane. Thus, lithornithids and kiwis do not need such a high medial patellar ridge to resist this medial vector. This, however, imparts a different stress on the knee. As the knee moves closer to the midsagittal plane, the medial collateral ligament experiences increasingly greater tension. Accordingly, the insertion for the medial collateral ligament is extremely deep in lithornithids.

Unequal elevation of the tibial condyles and tarsometatarsal cotylae in lithornithids results in movement of the tarsus away from the sagittal plane when it is flexed. The tibiotarsus and tarsometatarsus are parallel during tarsometatarsal extension, but the proximally elevated medial articular surfaces and more distal lateral articular surfaces direct the tarsometatarsus laterally during tarsometatarsal flexion.

The lithornithid tarsometatarsus has a large interosseous foramen, a condition that is most greatly exaggerated in jacanas (Jacanidae), to which the lithornithids otherwise bear little resemblance, particularly since their toes were not nearly so long. The large interosseous foramen is merely an indication that the fleshy belly of the extensor brevis digiti IV muscle is large and extends into the foramen. This muscle seems to have been opposed by an equally large antagonist, the flexor brevis digiti IV muscle, judging from the muscle scars on the tarsometatarsus. Similarly, there is a large scar left by the flexor brevis digiti II. Hence, in the leg, as in the wing, distal inertia is maximal.

The lack of the ossification of the tendinal bridge of the tibiotarsus and hypotarsal canals of the tarsometatarsus in lithornithids are, by comparison with Mesozoic avian and non-avian outgroups, almost certainly primitive characters (see Figs. 39 and 40). It is not clear whether osseous canals are less susceptible than are ligamentous retinacula to damage by the tendons that pass through them. Owls convergently lack these osseous canals, yet possess some of the most powerful legs of all birds. Furthermore, in all birds the tendon of the extensor digitorum longus muscle, which usually passes under an osseous bridge, has much the same morphological relationships as the tibialis cranialis muscle, which lies alongside it but is restrained only by the ligamentous extensor retinaculum. This is analogous to the condition in lithornithids and most ratites, in which the tendon of the extensor digitorum longus muscle is restrained only by a ligament. Thus, the lack of osseous canals in lithornithids is probably phylogenetically primitive, not funtionally adaptive.

The claws of lithornithids are large, strongly curved, and are probably adapted for perching in trees. They resemble the claws of tree-perching galliform birds (e.g., *Penelope*), not the relatively straight claws of strictly terrestrial galliform birds (e.g., *Meleagris*) or diggers (e.g., *Megapodius*).

NESTING BEHAVIOR

Many paleognathous birds exhibit a mating system of simultaneous polygyny by males and sequential polyandry by females (Meise, 1963). In this system, two or more females mate with and lay their eggs in the nest of a single male, which they leave in order to mate with other males. Consequently, clutch sizes are characteristically large, often being composed of dozens of eggs. The male is responsible for incubation and care of the chicks. Based on his interpretation of fossil embryos, Elźanowski (1985) considers this behavior, and male parental care in general, to be primitive in birds. Most authors disagree (see Skutch, 1976). In the vast majority of birds, both sexes, or only the female, incubate and rear the brood.

Fossils of *Lithornis* in calcareous nodules are typically found in association with large accumulations of eggshells that consistently resemble those of tinamous, both macroscopically and microscopically (Fig. 31). In all likelihood, these are correctly attributed to *Lithornis.* Although the number of eggs represented by the individual accumulations of eggshells is unknown, they obviously represent many eggs. Unfortunately, most of the eggshell is destroyed by acid preparation of the fossil bones; only exceptionally well-preserved eggs are saved.

The most plausible explanation for the occurrence of large accumulations of lithornithid eggshells is that individual clutches were large. The large accumulations of eggshell do not seem to be the result of coloniality because the bones of immature birds, so common on the floors of bird colonies, are rarely found associated with the eggshell and adult skeletons. The remains of other small vertebrates are frequently associated with the eggshell accumulations, suggesting that some degree of transportation and concentration was involved; thus, the caches were not actually nests, themselves. Since these were not nests, the possibility that the eggshells represent dump nests, as in waterfowl, or are analogous to the mounds of megapodes, is implausible. The association of the small vertebrates with the eggs cannot be readily explained as material brought to the nest by the birds because the lithornithids possessed relatively delicate probing bills, unlike the bills of predators. Nor is it likely that the eggshells were concentrated from more than one nest because they show no signs of abrasion and thus could not have been transported far. Assuming that lithornithids were not colonial, then it is unlikely that the eggshells from more than one nest should *typically* be preserved together. I believe that the caches of eggshell represent the contents of individual nests, but not the nests, themselves. Given that the polygamous mating system of simultaneous polygyny and sequential polyandry is peculiar to and prevalent among extant paleognathous birds, it is the preferred explanation for the accumulations of the fossil eggs. It is a shared behavioral character, uniting modern paleognaths as a monophyletic group (Meise, 1963), which was undoubtedly inherited from a common ancestor such as *Lithornis.*

Lithornithids exhibit so many characters that seem to be primitive for

birds that it would not be surprising if their presumed mating behavior was also primitive. However, the age of lithornithid fossils has no bearing on the question of whether male parental care was primitive or derived among birds. Other birds, such as owls, which were contemporaneous with lithornithids presumably did not exhibit this mating behavior.

PHYLOGENETIC ANALYSIS

RELATIONSHIPS OF THE LITHORNITHIDAE

Two decades ago a paleontologist's work was much simpler than it is today. Relationships of paleotaxa were determined on the basis of their overall similarity to modern forms. Within such a phenetic context, there is little doubt that the Lithornithidae would have been placed in the Tinamiformes, consistent with the ordinal classification of extant birds. Today, however, it is necessary to identify the polarities of the character states that are used to unite or separate taxa. The construction of cladograms is a useful exercise that helps to insure that character distributions are not mutually inconsistent. Since the determination of character state polarity is subjective, however, and because choosing between alternate phylogenetic reconstructions requires the invocation of convergence in one set of characters instead of another set, the conclusions drawn from this or any such study are subject to future testing, and are probably never really verifiable or falsifiable. The cladistic analysis of the Lithornithiformes is thus the most speculative and weakest aspect of this paper.

The familial relationship of the lithornithids, *Lithornis*, *Paracathartes*, and *Pseudocrypturus*, can be shown on the basis of shared derived characters (Figs. 39 and 40), as well as overall phenetic similarity. Lithornithids were a monophyletic clade, whether holophyletic or paraphyletic. Relationships within the Lithornithidae are not easily determined cladistically because the family is so uniform. The few characters that differ between species of *Lithornis* (e.g., tapered or truncate caudal ischium, curvature of the scapula, and breadth of the supraorbital region), vary in accordance with overall size of the species; thus, the nearest relations are probably between species of similar size. However, it is also possible that size-related differences, with developmental or functional origins, may be convergent and obscure "good" phylogenetic characters, instead. *Pseudocrypturus* shares more similarities (e.g., scapula relatively uncurved and caudal ischium more tapered) with *Lithornis*, possibly because these species are among the smallest lithornithids. *Paracathartes* and *Pseudocrypturus* both have short wings but *Paracathartes* shares some characters with *Lithornis* that *Pseudocrypturus* does not (e.g., palatal bones without caudal process, pterygoid fossa large, scapula robust and curved, and middle trochlea of the tarsometatarsus asymmetrical). *Paracathartes* probably inherited its ratite-like microscopic pattern of bone vascularization (and the possibly ratite-like cranium) from a true ancestor of ratites, assuming it was not itself directly ancestral to any ratites.

My decision to place the Lithornithidae in their own order is based in part on cladistic methodology and in part on my conviction that modern paleognathous birds are sufficiently diverse to be classified in at least two orders
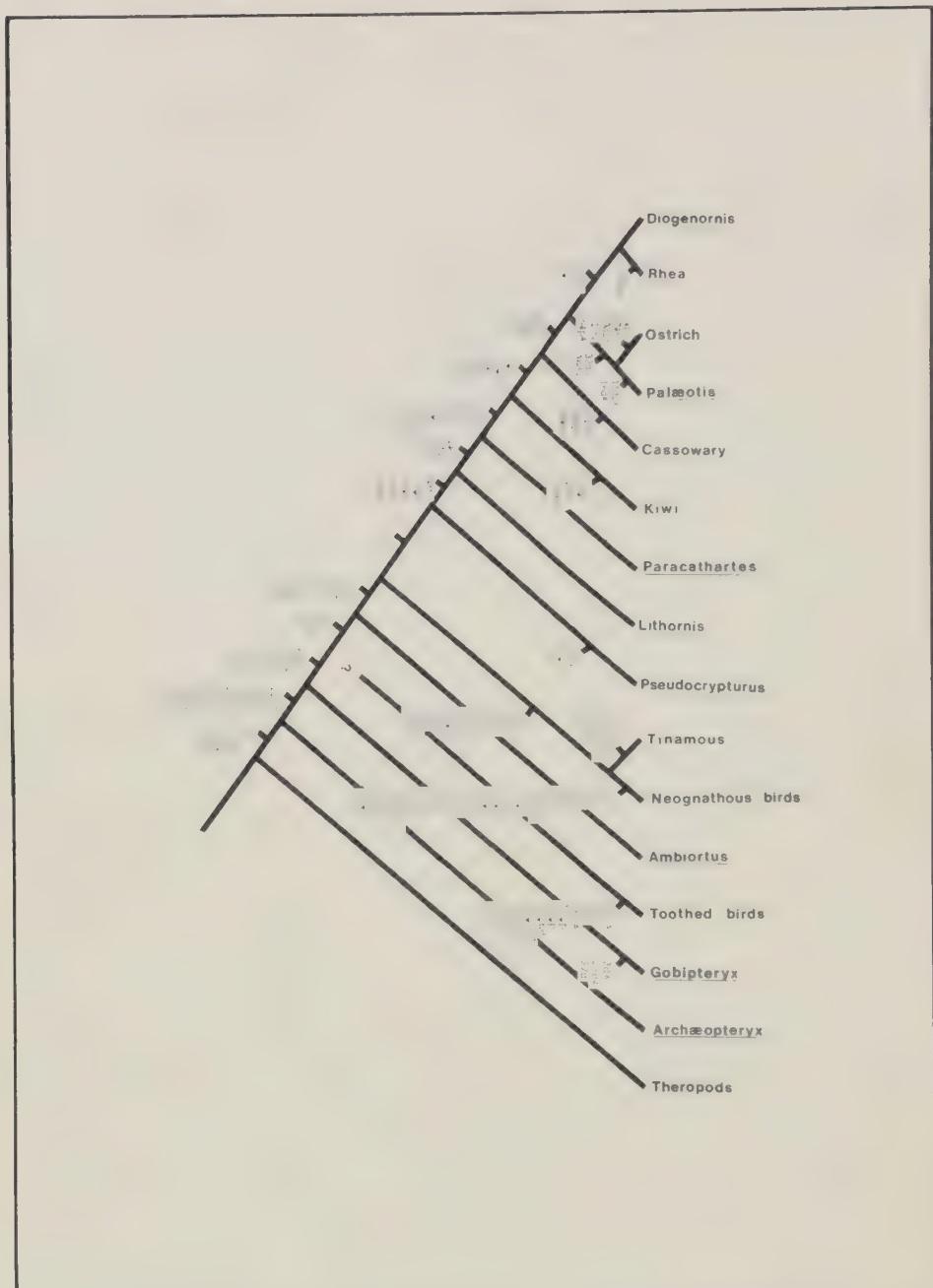
Fig. 39. Cladogram showing distribution of characters and states used in the phylogenetic analysis of paleognathous birds, neognathous birds, and primitive outgroups. Galliformes are assumed to be basal to neognathous birds and characters shared by Tinamiformes and Galliformes are assumed to be the result of common ancestry. See Table 27 (p. 104) for list of characters. Arrow indicates reversal to primitive state, triangle indicates convergence.
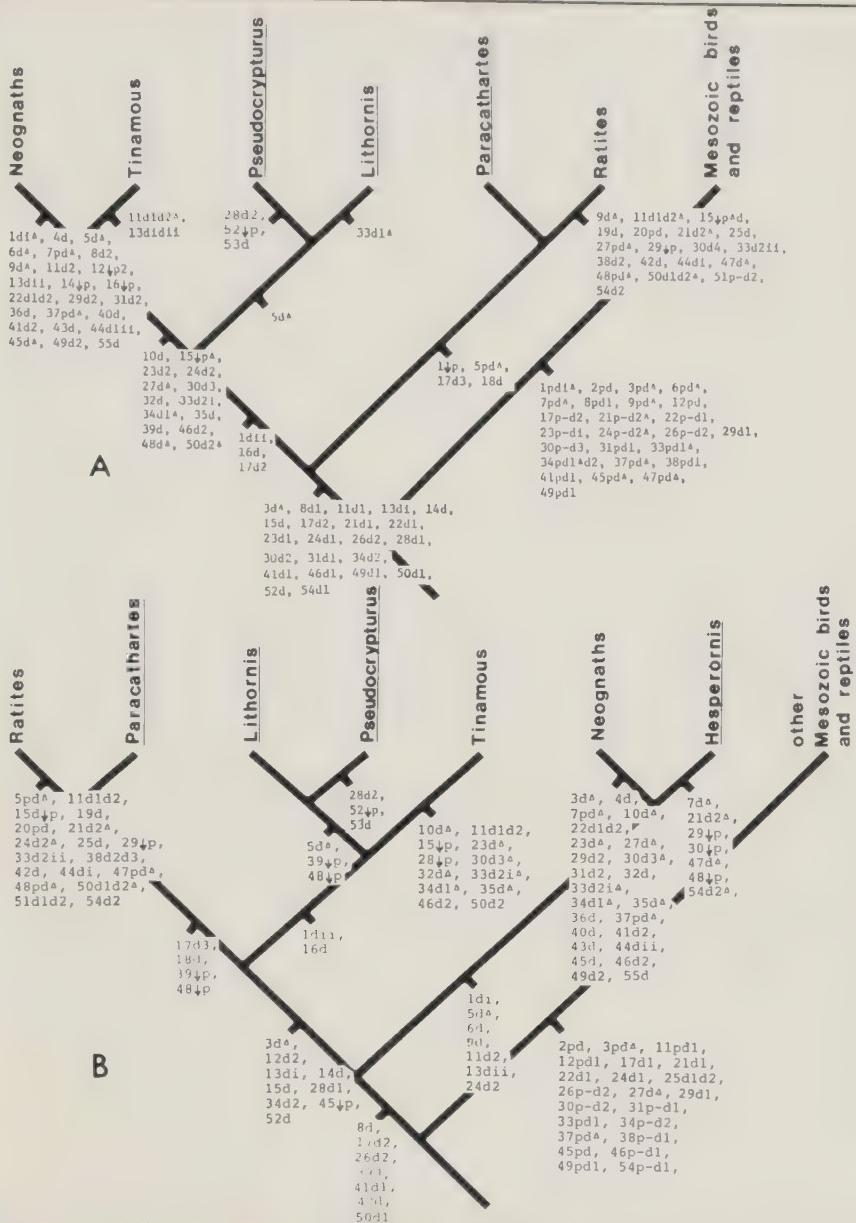
Fig. 40. Alternate cladograms that account for the distributions of character states differently than Figure 39. Neognathous birds refers to Galliformes, which are presumed to be basal to other neognathous birds. See Table 27 (p. 104) for list of characters. Arrow indicates reversal to primitive character state, triangle indicates convergence. 40a. The pattern of bone vascularization in neognathous birds and *Hesperornis* is convergent. 40b. There is no convergence in bone histology but most of the postcranial similarities of Tinamiformes and Galliformes are convergent; agrees with the phylogeny of paleognathous and neognathous birds advocated by Sibley and Ahlquist (1981, 1985), unlike Figures 39 and 40a.

(after Sibley and Ahlquist, 1981, *contra* Cracraft, 1981). Although I regard the similarities of tinamous and lithornithids to be the result of common ancestry, I also believe that lithornithids and ratites share a more recent common ancestry with each other than either do with tinamous (see below). According to strict cladistic methodology, the Lithornithidae should thus be included within the Struthioniformes. However, with no clearly *derived* characters to unite lithornithids with *all* ratites, I cannot advocate placing these birds in the same order.

The similarities of tinamous and lithornithids to each other only reflect very primitive morphologies, analogous to the greater phenetic similarity of *Hyracotherium* (Equidae) to other early ungulates than to extant horses. Other researchers may disagree with me, though, and separation of the Lithornithidae at the ordinal level will, I hope, avert controversy over whether the Lithornithidae should be placed within the Tinamiformes or instead within the Struthioniformes. In my opinion, lithornithids are sufficiently distinct ecologically from both ratites and tinamous to warrant their separation at the ordinal level.

The Lithornithidae might also be legitimately placed within the order Ambiortiformes of Kurochkin (1982) because *Ambiortus* and all lithornithids possess a uniquely styloid scapular acromion. The Lithornithidae cannot, in fact, be adequately differentiated from the Ambiortidae, but this is largely because *Ambiortus* is only known from very crushed and fragmentary remains. It has yet to be established, for example, that *Ambiortus* has a paleognathous palate. Additional fossil specimens will be needed before the affinity of the Lithornithidae and Ambiortidae can be confirmed.

The relationships of the lithornithids are clearly with the paleognathous birds. They possess all of the characters of the palate (Bock, 1963), rhamphotheca (Parkes and Clark, 1966), and pelvis (Cracraft, 1974) that have been used to define paleognathous birds. They are overall most similar to the tinamous because of the morphology of their neurocranium and hindlimb. However, they also share some important characters with the ratites, particularly kiwis. The combination of tinamou-like and ratite-like characters in these fossils provides the first paleontological confirmation of the affinity of modern paleognathous birds.

The phenetic intermediacy of lithornithids between tinamous and ratites (supporting the phylogenetic reconstruction in Figs. 1a and 1b) is most valuable in the determination of character state polarities within the Lithornithidae. Lithornithids share characters with tinamous that tinamous share with nothing else (listed below). They also share characters with the ratites, particularly kiwis, that ratites share with nothing else (listed below). One character suite must be primitive and the other must be derived—the problem is to decide which is which. Since ratites are derived with respect to their flightlessness (de Beer, 1956) and large size, they are considered here to be relatively more derived in most of the characters that they do not share with tinamous. Thus, the more ratite-like forms, particularly *Paracathartes*, are considered to be more derived within the Lithornithidae. Lithornithids are

apparently closer than tinamous to the ancestry of ratites and fit Parkes and Clark's (1966) description of the "proto-tinamou." The distribution of gross osteological characters in these birds and primitive outgroups, I feel, best supports a phylogenetic hypothesis in which: (1) paleognathous birds are basal in the class Aves; (2) tinamous are the sister group of neognathous birds; and (3) lithornithids are close to the ancestry of ratites (Figs. 1b and 39). This phylogeny, except for the sister group relationship of tinamous and gallinaceous birds, is congruent with immunological (Prager, et al., 1976; Prager and Wilson, 1980) and protein sequencing (Stapel, et al., 1984) studies.

Evidence for the sister group relationship of the Lithornithidae to the ratites comes from ratite-like cranial and histological characters that are present in some, but not all, lithornithids and that are absent altogether in tinamous (listed below). These ratite-like characters must have first evolved in the lineages that link the lithornithids that do not possess them with the lithornithids that do possess them. Lithornithids are thus paraphyletic, no longer holophyletic, since they (not necessarily any of the species described in this paper) were ancestral to some, if not all, of the ratites. Lithornithids are best treated as a single family regardless of their probable paraphyletic relationship with ratites, nevertheless, because the specific lithornithids that are included within the ratites depend upon which characters one chooses to define the ratites. For example, *Paracathartes* and ratites can be defined as a holophyletic clade, exclusive of *Lithornis* and *Pseudocrypturus*, on the basis of bone histology. *Paracathartes*, *Lithornis*, and ratites can be defined as a monophyletic clade, exclusive of *Pseudocrypturus*, on the basis of their possession of a large pterygoid fossa (secondarily lost in all extant ratites except kiwis, as demonstrated by its presence in *Palaeotis*, a primitive ostrich). All lithornithids can be grouped with the ratites on the basis of their derived quadrato-mandibular articulation (also secondarily lost by all extant ratites except kiwis).

Characters (both primitive and derived) that are shared by lithornithids and ratites but not shared with tinamous are as follows. Lithornithids and all ratites except moas (and some kiwis) (1) lack the osseous tendinal bridge of the tibiotarsus and (2) have a large occipital condyle. All lithornithids and kiwis share (3) femoral characters including the low trochanteric crest, centrally placed insertion of the iliotronchanteris caudalis muscle, and small medial condyle, and (4) characters of the feeding apparatus including specializations of the quadrate, mandible, internasal and intranasal septa, and large foveae of nervous corpuscles. *Paracathartes* and large ratites share (5) the concentric circular arrangement of vascular canals of the tibiotarsus and (6) possibly the large rounded postorbital process and large tympanic cavity forming the most caudal portion of the cranium. Most lithornithids share with cassowaries (7) vertebral characters and (8) the spiral groove of the humerus.

Clearly synapomorphous, versus symplesiomorphous, characters of lithornithids and some, but not all, ratites are restricted to the kiwi-like jaw

articulation and the palate with large pterygoid fossae (presumably lost secondarily by ratites other than kiwis), and probably the cranial and possibly the histological similarities of *Paracathartes* and ratites. Nevertheless, none of the known lithornithids is likely to have been ancestral to ratites because lithornithids are geologically young and because the premaxillae probably articulated with the vomer in true ratite ancestors, as they do in tinamous, many ratites, and probably *Pseudocrypturus*. The vomer-premaxillary articulation was presumably lost secondarily by lithornithids other than *Pseudocrypturus*.

Characters that are shared by tinamous and Galliformes but not shared by lithornithids are considered here to probably be synapomorphous to the tinamou-galliform group (Figs. 1b, 39, and 40a), although my phylogenetic reconstruction of the Lithorniformes does not rest entirely on the unverified hypothesis of tinamou-galliform relationship. I believe that Tinamiformes and Galliformes probably form a natural group because of their postcranial osteological similarities, for example the notarium and many others discussed at length in Chapter 4, pp. 107–117. Characters shared by tinamous and Galliformes are not considered to be symplesiomorphous because paleognathous birds, particularly lithornithids, share many characters with primitive outgroups that Galliformes do not (see below). The weakest aspect of the phylogenetic reconstruction depicted in Figure 40b is that most of the characters shared by Tinamiformes and Galliformes are assumed to have evolved independently through convergence. The notarium and osseous tendinal bridge of the tibiotarsus need not have evolved through convergence, though, if they were secondarily lost by non-tinamiform paleognaths. If the characters shared by Tinamiformes and Galliformes are, in fact, convergent specializations, the cladogram in Figure 40b probably more closely resembles the actual phylogeny of birds than any of the other reconstructions discussed in this paper. Convergence of Tinamiformes and Galliformes is not implicit in the topology of Figure 40b, however.

Obviously, the similarities of tinamous and gallinaceous birds and the similarities of lithornithids and Olson's (1985) "basal land birds," such as touracos, cannot both be truly indicative of kinship unless either paleognathous birds or neognathous birds are polyphyletic. Since neither is likely to be polyphyletic, there is at least some convergence in one or both of the pairs, tinamous plus gallinaceous birds and lithornithids plus basal land birds. Overall, the similarities of tinamous and gallinaceous birds are more numerous and more convincingly homologous than the similarities between lithornithids and "basal land birds." Thus, I prefer the hypothesis of a relationship of tinamous and gallinaceous birds. On the other hand, a few characters shared by lithornithids and basal land birds are also similar to the condition in tinamous, and these probably represent true symplesiomorphies. Truly primitive characters in neognathous birds probably include the sternum with few costal processes, the furcula that lacks a hypocleideum and articular facets for the coracoid, the knob-like bicipital crest of the humerus, and the pectineal process and deep ilioischiadic fossa of the pelvis.

Characters that are shared by lithornithids and tinamous, but neither by Galliformes nor ratites, are considered here to be symplesiomorphous in Figures 1b and 39, especially if they are shared by Mesozoic birds or reptilian outgroups. However, in Figures 1a, 40a, and 40b these shared characters are considered to include both primitive and derived states. These shared characters include (1) the caudal process of the palatine bones, (2) the vertebrae with narrow bodies, wide transverse processes, and deep pits medial to the anterior zygapophyses (although the vertebrae of lithornithids are somewhat intermediate between those of tinamous and some ratites), (3) humeral characters such as the knob-like bicipital crest and the configuration of the distal end of the humerus, especially the lack of tricipital grooves, and (4) characters of the carpometacarpus, especially the ventral location of the minor metacarpal. Large species of *Lithornis* and tinamous share (5) the caudally truncate ischium (rarely a tinamou will be found that possesses a caudally tapered ischium, e.g., a specimen of *Eudromia elegans*, UK 78028). In addition, lithornithids and tinamous of open country, like *Rhynchotus*, share (6) the pelvis with deep ilioischiadic fossae, (7) the relative lengths and morphology of the tibial cnemial crests, (8) the relative proportions of the appendicular elements of the pelvic appendage, and (9) characters of the tarsometatarsus. Forest-dwelling tinamous, such as *Eudromia*, and all sufficiently known lithornithids except *Paracathartes* share (10) cranial details, notably the absence of parabasal tubercles.

Characters present in lithornithids that I consider to be generally primitive avian characters because they are shared by reptiles or Mesozoic birds include (1) incomplete cranial fusion, (2) what seems to be the "foramen jugulare spurium" of Müller (1963) (= "post-temporal fossa" of Whetstone, 1983), (3) "basipterygoid processes" of the skull, (4) the large unfused splenial that contributes to the mandibular symphysis, (5) possibly the large foveae of nervous corpuscles of the mandibular nerve which previously may have innervated teeth, (6) the large occipital condyle, (7) the sternum with few costal processes and (8) coracoidal sulci that cross in the midline, (9) the furcula that lacks a hypocleideum and (10) lacks articular facets for the coracoid, (11) the humerus with a knob-like bicipital crest and that (12) lacks tricipital grooves, (13) the scapula with a long pointed acromion, (14) a muscular antebrachium, (15) lack of fusion between the innominates and synsacrum, (16) the open ilioischiadic foramen, (17) lack of a well-developed pygostyle, (18) lack of an osseous tibial tendinal bridge, (19) tarsometatarsus with a simple unperforated hypotarsus, (20) the muscular tarsometatarsus, and possibly (21) male parental care.

Lithornithids even share some characters with Mesozoic birds or reptiles that tinamous do not, further supporting my interpretation of character polarity in lithornithids, tinamous, and Galliformes. These characters include (1) the large occipital condyle (cf., reptiles), (2) the sternum with coracoidal sulci that cross the midline (cf., *Ichthyornis*), (3) the styliform acromion (cf., *Ambiortus*), and (4) lack of an osseous tibial tendinal bridge (cf., reptiles, *Archaeopteryx*, *Ichthyornis*, and *Hesperornis*). The pattern of

microvascularization in the tibiotarsi of ratites (Amprino and Godina, 1944; Zavattari and Cellini, 1956) and *Paracathartes* (Houde, 1987a) is similar to that described for a few dinosaurs (Madsen, 1976; Ricqlés, 1981; Reid, 1985). A word of caution here, though. I found *Hesperornis* to possess the same randomly branching and anastomosing pattern of bone vascularization in its tibiotarsus as is typical of neognathous birds and unlike the patterns typically found in paleognathous birds (Houde, 1987a). Moreover, this pattern is seemingly not correlated with functional adaptation because all the neognathous birds I examined exhibited the same pattern, whether the species were flightless or volant, large or small, or the individual young or old. This suggests that some seemingly primitive characters may have evolved by way of reversal from a derived back to a more primitive condition. Similarly, according to the inter-ratite phylogeny advocated by Sibley and Ahlquist (1981, 1985), the osseous tendinal bridge of the tibia has either been convergently evolved or independently lost by at least some paleognathous birds, and therefore the interpretation of its absence as primitive is questionable.

The phylogenetic reconstruction that I think is best supported by the gross morphology of the fossils (Fig. 39) does not accord well with phylogenetic reconstructions generated from molecular evidence (neither do Figs. 1b and 40a). Note, however, that it is the sister group relationship of tinamous and Galliformes, neither the sister group relationship of lithornithids and ratites nor the primitiveness of paleognathous birds, that is in conflict with the molecular studies. But, molecular systematists are not in complete agreement about the relationships of these birds, either. Stapel, et al. (1984) advocate that the earliest divergence among Aves was between the paleognathous birds and the neognathous birds, so tinamous and ratites are sister taxa, on which Prager, et al. (1976), Prager and Wilson (1980), and Sibley and Ahlquist (1981, 1985) agree. In this hypothesis, paleognathous birds and neognathous birds could both be holophyletic or either could be paraphyletic if all extinct taxa are included. Sibley and Ahlquist (poster: XIXth International Ornithological Congress, 1986, Ottawa) maintain that the oldest divergence in Aves was within neognathous birds. If so, then *modern* neognathous birds are paraphyletic, as they were ancestral to the holophyletic paleognathous birds. The phylogenetic hypotheses presented in Figures 1a, 1b, 1c, and 40b accord with the hypotheses based on the molecular data.

I do not view discrepancy between the phylogeny I prefer on the basis of anatomical data and those derived from molecular evidence as a major problem, for several reasons. The phylogenetic reconstructions I have proposed are merely hypotheses that attempt to best explain the distribution of morphological character states I have observed. The same can be said for reconstructions based on molecular evidence; each provide the best estimate of phylogeny given the particular data observed. They don't all agree with one another, either (e.g., see branching order of ratites in Prager and Wilson, 1980). Whereas molecular techniques are powerful tools for estimating

phylogeny, they are subject to ambiguity in interpretation, as are other methods (Houde, 1987b, c). In particular, the relationship of paleognathous and neognathous birds propounded by Sibley and Ahlquist (1981, 1985) was put forth with the assumption that rates of molecular evolution were uniform across all avian taxa. The clustering algorithms they used required that this be true. This notion has since been put to rest (Houde, 1987b) and it is unclear how these authors will treat the paleognathous birds with new analytical tools. Three other factors could potentially contribute to misinterpretation of the DNA distance data. (1) The split between the lithornithid-ratite group and the tinamou-neognath group, while forming a major morphological dichotomy in my Figure 1b, is phylogenetically minor compared with the great radiations within the ratites and especially the neognathous birds. The branch lengths between the origin and the tinamou-neognath and lithornithid-ratite dichotomies may be very short in terms of real time and thus might be undetectable by the DNA hybridization technique. (2) The genetic distances between paleognathous and neognathous birds are extremely large, approaching the limit of resolving sensitivity of the DNA hybridization technique. (3) Relative rates of evolution can only be evaluated by comparing the genetic distances of a pair of sister taxa (paleognathous and neognathous birds, in this case) to some outgroup. Hybridization comparisons at this high taxonomic level may be beyond the resolution of the DNA hybrization technique.

HYPOTHESIS OF PALEOGNATH HOLOPHYLY

In the past, arguments for the monophyly of paleognathous birds have centered around the distinctiveness of paleognathous birds as evidence of phylogenetic closeness. The interpretation of paleognathous birds as "derived" gains its greatest strength from the observation that ratites are "derived" as flightless birds. Thus, they were treated (e.g., Cracraft, 1973) as though they are derived in all characters. Indeed, I used the same logic in this paper to establish polarity of character suites among paleognathous birds and, in turn, Lithornithiformes. Bock's (1963) assertion that paleognathous birds are holophyletic is, however, specifically based on his analysis of the feeding apparatus. Arguments against the monophyly of paleognathous birds have been more concerned with the obvious potential for convergence in the flightless "ratite" condition and the primitiveness or neoteny of the paleognathous palate itself (Feduccia, 1980; Houde and Olson, 1981). But, what is hypothetically plausible should not, therefore, be accepted as fact. Extant ratites, if not all paleognathous birds, are each other's closest relatives (Prager, et al., 1976; Prager and Wilson, 1980; Sibley and Ahlquist, 1981, 1985; Stapel, et al., 1984), but it is not clear whether neognathous birds gave rise to paleognathous birds, or vice versa, or neither. Thus, the following discussion is not confined to the question of whether the extant paleognathous birds are monophyletic, but considers whether the Palaeognathae, including extinct forms, are holophyletic or paraphyletic. Lithornithid

fossils support the monophyly of all paleognathous birds, contrary to the original interpretation of Houde and Olson (1981), which preceded the DNA hybridization studies and the recognition that lithornithids combine the characters of both ratites and tinamous.

Bock (1963, 1964) enumerated the similarities in the palatal complex of bones of paleognathous birds, and argued that all of these characters are homologous. He interpreted this homology as a complex of shared derived characters that could be used to unite all paleognathous birds as a "strictly monophyletic" (=holophyletic) group. His conclusion that the paleognathous palate was derived rather than primitive among Aves was based on the degree of similarity of the palates of these birds, together with his hypothesis for the evolution of paleognathous rhynchokinesis from neognathous prokinesis from mesokinesis in *Archaeopteryx*. The reconstructions of the skull of *Archaeopteryx* upon which Bock relied are no longer accepted as correct (Bühler, 1985); *Archaeopteryx* was not mesokinetic. The coronal suture would have to be two dimensional to permit kinesis, but it is three dimensional in *Archaeopteryx*, and, thus, could not have been kinetic. The same argument against mesokinesis is valid in lithornithids (*contra* Houde and Olson, 1981). This does not mean that Bock's conclusions were incorrect, but his progression of logic was unfortunately flawed from the start.

If it could be convincingly demonstrated that the paleognathous palate, or any other character of paleognathous birds, were synapomorphous rather than symplesiomorphous, then it would logically follow that paleognathous birds are holophyletic, as per Bock (1963, 1964). The paucity of extant paleognathous birds and the degree of similarity of their palates do not, however, rigorously demonstrate the synapomorphy of the paleognathous palate. Outgroup comparisons suggest the opposite polarity in several of the characters that form the paleognathous complex (Cracraft, 1986).

Lithornithid fossils unfortunately provide no new direct evidence on the primitiveness or recency of the paleognathous palate itself. The age of the lithornithid fossils is insufficient to argue for primitiveness of their palatal morphology; many neognathous birds were contemporaneous with lithornithids. However, lithornithid fossils do provide a wealth of other evidence that supports the primitiveness of paleognathous birds, particularly the characters shared by lithornithids and reptiles or Mesozoic birds.

Any characters that are shared by lithornithids and Mesozoic birds or reptiles but not shared by basal neognathous birds either (1) evolved convergently in lithornithids (i.e., paleognathous birds evolved from neognathous birds) or (2) were inherited by lithornithids and lost in the basal neognathous birds (i.e., neognathous birds evolved from paleognathous birds). Galliformes are treated here as basal neognathous birds, based on their immunological (Prager and Wilson, 1980) and eye-lens protein sequence (Stapel, et al., 1984) disparity from other neognathous birds together with the assumption that the similarities they share with Tinamiformes are due to common ancestry rather than convergence. The primitive characters shared by paleognaths and Mesozoic birds or reptiles but, in general, not neognathous

birds are listed on page 127. In contrast, there are no characters of which I am aware, except the paired clavicles of touracos, that are shared by neognathous birds and primitive outgroups that are not also shared by lithornithids. Thus, cladistic analysis of osteological evidence supports the primitiveness of paleognathous birds. The similarity and paucity of paleognathous birds does not support the synapomorphy of the characters they share.

The distribution of these characters together with the reptilian appearance of the paleognathous palate itself should be sufficient to cast strong doubt on Bock's hypothesis that paleognathous birds are derived from neognathous birds. However, the rhamphothecal grooves of Parkes and Clark (1966) remain as one morphological character that unites all paleognathous birds and that is not present in any known primitive outgroups, except possibly *Gobipteryx* which has foveae of nervous corpuscles arranged in a line where the grooves would otherwise be located.

VICARIANCE BIOGEOGRAPHY HYPOTHESIS OF RATITE ORIGINS

Cracraft's (1973, 1974) vicariance biogeography hypothesis presumes that ratites are each others' closest living relatives, following Bock (1963, 1964). He interprets the geographic distribution of ratites as an indication of the age and distribution of the common ancestor of ratites. The relative order of divergence of the various ratite lineages were hypothesized on the basis of cladistic analysis of osteology (Cracraft, 1974) and genetic distances derived from microcompliment fixation (Prager, et al., 1976) and DNA hybridization (Sibley and Ahlquist, 1981, 1985). These authors found, in most cases, that the branching order of the ratite lineages approximate the relative order of isolation of the component continents of the ancient supercontinent Gondwanaland, even though they disagreed on some of the branching orders. It is generally accepted that the ratites evolved from volant ancestors, as argued by de Beer (1956), although this is still debated (McGowan, 1982). Embracing the parsimony criterion, proponents of the vicariance biogeography hypothesis of ratite origins, propose that the common ancestor of all ratites was already flightless and that flightlessness did not evolve convergently in the different ratite lineages. Populations of this flightless pluripotent ratite ancestor already present in Gondwanaland, they say, were isolated by ocean barriers as they arose. Ratites are viewed as passive passengers on rifting continents; populations isolated and diverged as daughter continents were born. The present-day distribution of ratites is due only to the distribution of this flightless ancestor in Gondwanaland and the subsequent breakup of this ancient supercontinent to form the existing Southern Hemisphere landmasses.

The dating of the "DNA molecular clock" is largely based on this hypothesis. Sibley and Ahlquist (1981, 1985) maintain that the divergence of ratite DNA sequences was initiated by and, therefore, can be dated by the rifting of Gondwana. More significantly, they have applied this temporal

calibration of genetic distance to a variety of other organisms (Sibley and Ahlquist, 1983, 1984; Houde, 1987b).

The vicariance biogeography hypothesis of ratite origins can be tested by rejection if ratites are either shown to have evolved flightlessness more than once, to have evolved flightlessness after the vicariance of Gondwanaland, or to have evolved flightlessness anywhere other than in Gondwanaland. Although a ratite ancestor could have hypothetically dispersed to Gondwanaland after having evolved flightlessness elsewhere, this would not accord with this hypothesis as it is stated.

This study and other new paleontological work provide evidence both for and against the hypothesis of ratite origins in Gondwanaland. Support for the hypothesis comes from the recent discovery of an advanced ratite, *Diogenornis* (Alvarenga, 1983), in the late Paleocene of Brazil. *Diogenornis* shows that the geologically younger paleognathous taxa from the Northern Hemisphere that are described in this paper could not have been ancestral to any extant ratites unless the ratite grade was evolved more than once by paleognathous birds. If ratites, in fact, evolved flightlessness only once, then the early appearance of *Diogenornis* suggests that this could have occurred early enough to accord with a Gondwana origin of ratite birds, even though *Diogenornis* is not contemporaneous with the breakup of Gondwanaland. (An undescribed Miocene fossil, PA 36, intermediate between *Diogenornis* and rheas, provides evidence that *Diogenornis* was indeed close to the ancestry of modern rheas and is, therefore, relevant to this discussion).

Martin's (1983) interpretation of *Remiornis*, from the late Paleocene of France, as a ratite might provide further support for the great age of ratite birds. However, Martin did not indicate that *Remiornis* was related to any particular extant ratite or group of extant ratites. Paleognathous birds may have become secondarily flightless as many times as neognathous birds. Thus, the relevancy of *Remiornis*, or any other flightless birds, to the question of ratite origins is entirely dependent on the ability to demonstrate an ancestor-descendant relationship to extant ratites.

The close similarities of *Diogenornis* to both *Palaeotis* and cassowaries and the similarities of *Palaeotis* to both cassowaries and ostriches suggest that these birds really are related to each other, perhaps closely enough for flightlessness to have been derived only once in the evolution of ratite neospecies. In other words, the assumption of the Gondwana hypothesis that ratites are holophyletic and evolved flightlessness only once is supported by these ratite fossils (assuming that whatever is true for cassowaries is also true for all the Papuan-Australian-New Zealand ratites).

Even with the support that *Diogenornis* lends to the Gondwana hypothesis of ratite origins, conclusive evidence for this biogeographical hypothesis is still wanting and there remain major problems with this hypothesis. (1) Ancient as *Diogenornis* is, it is still about 30 million years shy of the age when South America rifted away from the remainder of Gondwanaland. (2) Sibley and Ahlquist's (1981) data from DNA hybridization indicate that kiwis did not diverge from the other ratites early enough to have inhabited

New Zealand when it first broke off from Gondwanaland. (3) *Palaeotis* appears to be a direct ancestor of or to be close to the ancestry of ostriches and to have evolved directly from lithornithid ancestors (Houde, 1986).

The origin of ostriches from lithornithid stock provides a viable alternative to the hypothesis of ratite origins in Gondwanaland. *Palaeotis* exhibits characters that are derived in the Lithornithidae and found nowhere else among paleognathous birds, i.e., palate with caudal processes of the palatine bones *and* pterygoid fossa, and tarsometatarsus with conspicuously concave origin of the extensor digiti IV brevis muscle and large interosseous foramen. Despite the fact that *Palaeotis* strongly resembles cassowaries, this is only because both retain many primitive characters (e.g., narrow bill and three toes), the symplesiomorphy of which can be demonstrated by outgroup comparison with lithornithids and tinamous. *Palaeotis* also possesses derived characters that define it as an ostrich (e.g., long humerus and short antebrachium, non-pneumatized humerus, carpometacarpus with accessory foramina between each of the metacarpals, and configuration of the scapulocoracoid) but none of the derived characters that define the cassowary-emu clade (e.g., caudal fusion of the ilium and ischium).

Volant birds have been immigrating to New Zealand throughout its history, thus kiwis and moas may have arrived as volant forms as well. The divergence time of kiwis from other paleognathous birds as indicated by DNA hybridization (Sibley and Ahlquist, 1981) does not accord with the very early separation of New Zealand from the Gondwana mother-continent (Fleming, 1975). It is generally accepted that the absence of land mammals in New Zealand results from New Zealand's divergence from Gondwana before mammals, as we know them, evolved. But modern mammals appear at least as early as, if not earlier than, birds in the fossil record (Novacek, 1982; Olson, 1985). Birds are therefore even less likely than mammals to have been passive passengers on mobile New Zealand at the beginning of its journey. Rather, kiwis probably flew there like all the rest of New Zealand's birds (including other secondarily flightless taxa) and mammals. If kiwis are the most recent paleognaths to have become flightless then there is little wonder that they retain so many more of the primitive characters exhibited by lithornithids than do any other ratite birds.

The possibility that kiwis could evolve the ratite morphology convergently is supported by the fact that some neognathous birds, such as *Gastornis*, have convergently evolved such characteristically ratite-like traits as the keel-less sternum, fused scapulocoracoid, and cassowary-like, elongate ilioischiadic foramen. These traits are presumably reversals to more primitive conditions and for this reason are probably more easily evolved through convergence (this may explain the fact that accessory foramina between the metacarpal bones are to be found among the carpometacarpi of some penguins [Spheniscidae] as well as in ostriches and *Palaeotis*). Furthermore, this convergence can come about very rapidly. *Thambetochen*, a subfossil flightless goose from Hawaii, evolved a nearly ratite grade of scapulocoracoid fusion possibly within five million years.

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If kiwis achieved the ratite grade independently, then this grade was evolved at least twice by extant paleognathous birds. This hypothesis does not conflict with Sibley and Ahlquist's (1981, 1985) phylogenetic reconstruction of paleognathous birds based on genetic distances because their phylogeny contains no information about morphology. Sibley and Ahlquist assume *a priori* that the paleognathous palate is derived and that ratites evolved flightlessness only once. If ostriches and rheas share a more recent ancestry with each other than with other paleognathous birds, as per Sibley and Ahlquist (1985), then they could share flightlessness as an inherited trait independent of other paleognathous birds. On the other hand, if cassowaries inherited flightlessness from the same ancestor as ostriches and rheas, then so did kiwis and emus. This follows because kiwis and emus shared a more recent common ancestry with cassowaries than they did with ostriches and rheas, according to the DNA hybridization study.

The DNA hybridization studies of Sibley and Ahlquist (1981, 1985) are valuable to the extent that they provide information on the relative divergence times for tinamous and ratites. However, there are problems in using genetic distances between ratites together with geological dates for the breakup of Gondwana in order to calibrate genetic distance with absolute time. The first problem is the mixed support that fossils provide for Cracraft's (1974) biogeographic hypothesis of ratite origins in Gondwanaland, upon which the calibration of the molecular clock is based. The second problem is the applicability of a calibration based on ratites to other taxa. If rates of evolution differ in different lineages of birds (Houde, 1987b, c; Sheldon, 1987), then the ratite clock will not necessarily keep time for any other organisms.

6

CONCLUSIONS

The Lithornithidae were a family of paleognathous carinate birds, currently represented by eight species in three genera, known from the late Paleocene to middle Eocene deposits of North America and Europe. Some species of Lithornithidae were incorrectly described as the earliest representatives of certain families of neognathous birds, such as the Threskiornithidae, Rallidae, Cathartidae, and Musophagidae, which are otherwise unknown from such ancient deposits.

Lithornithids had sensitive bills for probing and were capable of snipe-like distal rhynchokinesis. In general, lithornithid flight was intermediate between that of ibises and more obligatory soarers, such as the vultures (Vulturidae), and probably was characterized by slow, powerful wingbeats and intermittent periods of gliding. Short-winged lithornithids, however, particularly the turkey-like, heavy-set *Paracathartes*, were perhaps incapable of long-sustained flight. The tinamou-like tail of lithornithids was ridiculously short for relatively long-winged birds. Most lithornithids had legs and toes of similar proportions to those of tinamous, but their claws were quite hooked and suitable for perching in trees. Lithornithids seem to have had the same mating system of simultaneous polygyny and sequential polyandry that is common among many modern paleognathous birds.

Lithornis and *Pseudocrypturus, Paracathartes, Palaeotis, Diogenornis,* and extant ratites represent consecutive grades of ratite evolution that can be summarized as follows (Fig. 41):

1. The *Lithornis-Pseudocrypturus* grade: sustained fliers; neurocranium tinamou-like with small postorbital processes, small tympanic cavities, and short prefrontal bones, but with a large occipital condyle; viscerocranium kiwi-like with extensive ossification of nasal membranes, quadrate articulating in a notch formed posteriorly by the retroarticular process of the mandible, large pterygoid fossa *and* caudal process of palatine (both are not known together in any individual species of Lithornithidae), a "W" shaped pattern of rhamphothecal grooves on the ventral surface of the rostral mandible, and a sensitive bill; cervical vertebrae tinamou-like; sternum with few costal processes; scapular acromion long and pointed; humerus with knob-like bicipital crest and spiral groove, but lacking tricipital grooves; antebrachium relatively short and muscular; ulna with short olecranon process and flattened distal end; radius with broad asymmetrical distal condyle; pelvis relatively narrow with open ilioischiadic foramen and ventrally placed acetabulum; femur relatively long and tarsometatarsus short; femur with low trochanteric crest and centrally placed insertion of the iliotrochanteris caudalis muscle; tibiotarsus tinamou-like with longitudinally parallel microscopic vascular canals but lacking the osseous tendinal bridge; tarsometatarsus with knob-like hypotarsus, pro-
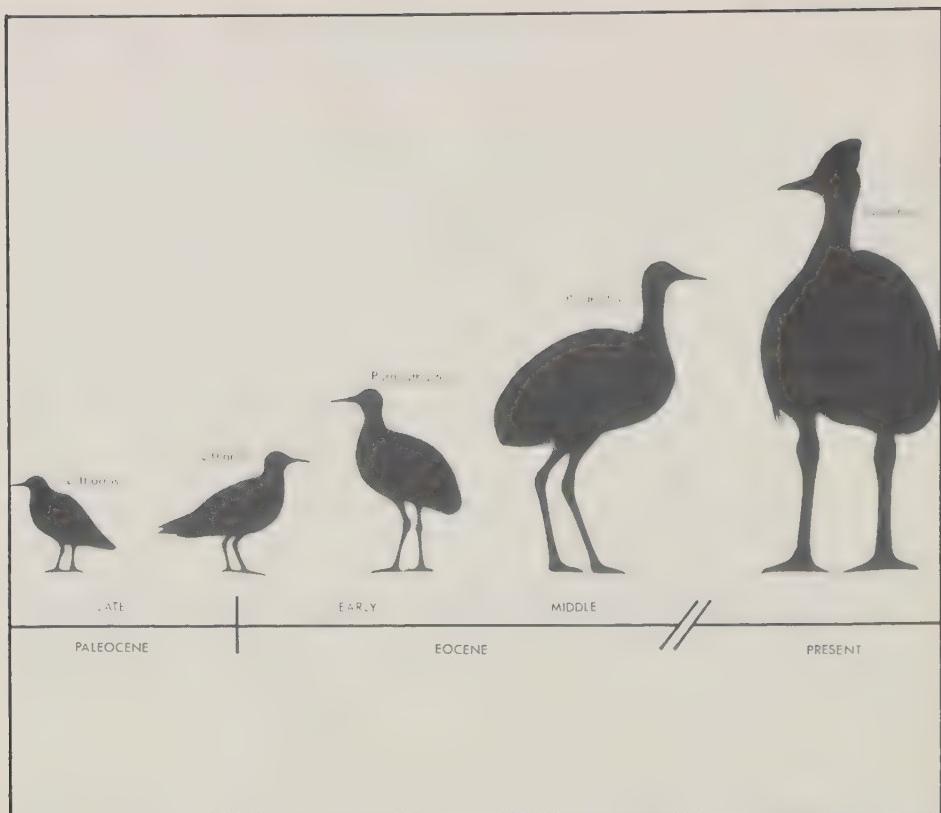
Fig. 41.   Grades of ratite evolution as represented by the series of fossils *Lithornis celetius, Lithornis promiscuus, Paracathartes howardae, Palaeotis weigelti,* and a modern cassowary (*Casuarius*), to scale. This figure does not imply any phylogenetic continuity or specific ancestor–descendant relationship of these particular taxa.

nounced spherical intercotylar eminence, deeply concave infracotylar region, deeply sculptured origin of the extensor digiti IV brevis muscle, and large interosseous foramen; digits well developed, four in number; eggs glossy with large, widely spaced pores and neither pole narrowed; and mating system polygamous.

2. The *Paracathartes* grade: larger, heavy-set, poor fliers; neurocranium possibly cassowary-like with large rounded postorbital process and large caudally pronounced tympanic cavity (see pages 42 and 48); viscerocranium kiwi-like, like that of *Lithornis,* with large pterygoid fossa and no caudal process of the palatine; cervical vertebrae intermediate between tinamous and cassowaries; pectoral girdle and appendage as in the *Lithornis* grade but elements relatively shorter and more robust; pygostyle rudimentary; pelvic appendage as in the *Lithornis* grade; tibiotarsus with longitudinally parallel microscopic vascular canals arranged in discrete concentric circular pattern; and hallux slightly reduced.

CONCLUSIONS

3. The *Palaeotis* grade: completely flightless birds, smaller than any extant ratites except kiwis; bill narrow and *Lithornis*-like with "W" shaped rhamphothecal grooves; viscerocranium still as in the *Lithornis-Pseudocrypturus* grade; prefrontal bones long and emu-like; sternum without keel; scapulocoracoid diminutive, fused, and with large lithornithid-shaped acromial region and pronounced acrocoracoid process; humerus long and spindley, and not pneumatized; antebrachium short; carpometacarpus with ostrich-like accessory foramina between each of the metacarpals; pelvis cassowary-like and bilaterally compressed; femur very short and tarsometatarsus long; tarsometatarsus with cassowary-like streamlined hypotarsus but lithornithid-like spherical intercotylar eminence, deeply concave infracotylar region, deeply sculptured origin of the extensor digiti IV brevis muscle, and large interosseous foramen; and foot tridactylous.

4. The *Diogenornis* grade: still larger; bill still narrow; tibiotarsus still with cnemial crests of tinamou proportions, condyles in medial and lateral views still like tinamous, lithornithids, and kiwis but in anterior view rhea-like with low proximal profile of condyles; tarsometatarsus still with deeply concave infracotylar region and large interosseous foramen but less distinct spherical intercotylar eminence.

Tinamous still exhibit many of the characters of the *Lithornis-Pseudocrypturus* grade of paleognathous birds but are apparently further along the lineage leading to neognathous birds; kiwis seem to be derived directly from the *Paracathartes* grade; cassowaries are little changed from the *Palaeotis* grade but do not possess the struthionid characters that distinguish *Palaeotis* as an ostrich; and rheas are far removed from but, nevertheless, probably derived from the *Diogenornis* grade (see page 132). In all the extant ratites, the interosseous foramen of the tarsometatarsus is small but this is apparently convergent with the condition in tinamous because all of the lithornithid and ratite fossils discussed here have large interosseous foramina.

The above series of fossils representing grades of ratite evolution suggests that if the power of flight was lost by paleognathous birds more than once, then these geologically young, North American forms could be ancestral to some extant ratites, in contradiction to Cracraft's (1973, 1974) hypothesis of ratite origins from a single flightless ancestor in Gondwanaland. Doubt is thus cast upon the validity of the dating of the "DNA molecular clock" (Sibley and Ahlquist, 1981, 1983) because it is largely based on the calibration of genetic distances between ratites against the geological dates for the vicariance of Gondwanaland.

Cladistic analysis using primitive outgroups in addition to extant avian outgroups points to the primitiveness of paleognathous birds. It is, however, as yet impossible to clearly disprove Bock's hypothesis of paleognath holophyly based on the synapomorphy of the paleognathous palate in birds. Additional evidence for or against this hypothesis will probably become available from new paleontological studies.

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